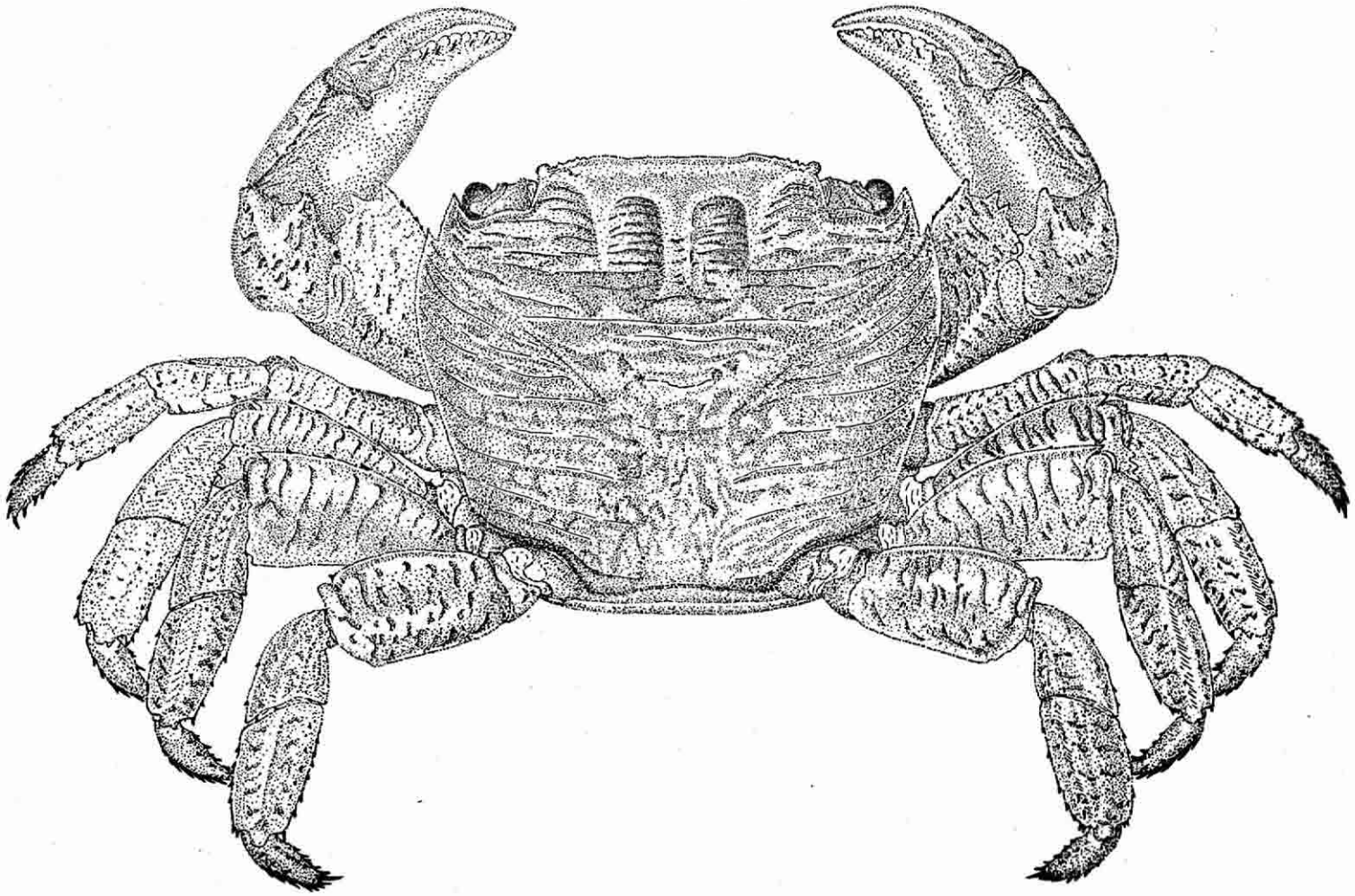

Pachygrapsus crassipes Randall. (Dorsal view of female, × 2.5.)

The Biology of the Lined Shore Crab, *Pachygrapsus crassipes* Randall

ROBERT W. HIATT[1]

INTRODUCTION

THE CONSPICUOUS LACK of knowledge of the natural history of littoral Brachyura (true crabs) of the west coast of North America has for a long time indicated the necessity for an investigation into the biology of a common and well-known decapod, such as the subject of this study, *Pachygrapsus crassipes* Randall (Frontispiece). This investigation has been designed to fulfill this need in part and has been pursued primarily from the ecologic and behavioristic points of view. A considerable portion of this paper has been devoted to the description of the molt and intermolt cycle of *P. crassipes.* Some recent data which have appeared in the literature have dealt with the extremely significant molt and intermolt cycles of the cancroid and oxyrhynchoid crabs, but the grapsoid group, to which *P. crassipes* belongs, has been neglected. Therefore, the present study, which includes comparable work on this grapsoid crab, materially extends the knowledge of these subjects within the group Brachyura. Included here, also, is a brief discussion treating the problem of the transition in the Brachyura from a marine habitat to a semi-terrestrial or amphibious existence. Among littoral Brachyura on the northern California coast, *P. crassipes* ranges highest along the shore and exhibits certain patterns both physiologically and behavioristically illustrative of this significant landward movement.

A primary aim has involved recording of field observations which have logically preceded laboratory investigations. Such field observations have provided the natural basis for the present laboratory studies, making the latter far more interesting and significant. On the other hand, clues to certain behavior patterns were exhibited among the captive crabs prior to their observation in the natural environment. In addition, the correlation of laboratory data with field observations has helped to illuminate certain behavior patterns, not only of *P. crassipes,* but of Brachyura in general, which have heretofore been incompletely known. It has not been the intention of the author to study exhaustively the multitude of morphological and behavioristic phenomena associated with this species. Rather, an attempt was made to become better acquainted with the behavior of the crab in question, with the underlying phenomena involved, and thus with the Brachyura in general.

Most of the knowledge of the natural history of decapod crustaceans stems from a series of studies upon those with economic value, although for diverse reasons these studies have subordinated natural history data in favor of securing information on life histories. The early literature is filled with abbreviated note-type accounts, but the more extensive investigations of H. C. Williamson on *Cancer pagurus* Linné, reported at the turn of the century (1899), were the first to provide substantial knowledge concerning any one decapod crustacean. Shortly thereafter Hay (1905) published "The Life History of the Blue Crab," in which he contributed much to the natural history of this species. Pearson (1908), in addition to his own investigations on *C. pagurus,* included

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Williamson's earlier findings, and in so doing provided the first comprehensive study of a crab. In 1909 Herrick summarized many years of research in a classic monograph on the American lobster, *Homarus americanus,* which for the past 35 years has stood unparalleled in the field. In 1915 the natural history and behavior of the fiddler crab were presented by Schwartz and Safir, and in 1918 Churchill amalgamated all the information on the life and natural history of the blue crab, *Callinectes sapidus* Rathbun, into a single authoritative report. In 1930 MacGinitie published an account of the natural history of the mud shrimp, *Upogebia pugettensis* (Dana), which was followed by a similar paper (1934) on *Callianassa californiensis* Dana. These investigations provided the first consequential studies of any west coast decapod crustacean which was unimportant economically. A series of studies throughout the past quarter century on the life history, growth, and migration of the Pacific edible crab, *Cancer magister* Dana, by Weymouth (1917), by the same author in collaboration with MacKay (1934, 1935, 1936), and by the latter author (1942), has furnished considerable significant information. More recently, Broekhuysen (1936) published an account of the development, growth, and distribution of a common European shore crab, *Carcinides maenas* (Linné). This was followed in 1941 by his similar investigation of the South African shore crab, *Cyclograpsus punctatus* M. Edwards. Other literature of a more specific nature will be discussed where pertinent in the text of this report.

In the voluminous literature dealing with the decapod Crustacea, only a few brief notes on the habits of the crabs of the genus *Pachygrapsus* can be found, and these furnish extremely few data on *P. crassipes.*

Acknowledgments: The writer is especially indebted to the late Dr. S. F. Light, of the Department of Zoology at the University of California, whose valuable assistance and helpful criticisms were most useful in the pursuance of this study. Special credit is also due to Dr. L. E. Noland, of the Department of Zoology at the University of Wisconsin, for many suggestions. I should like to express my gratitude to Dr. E. Yale Dawson, who provided identification of the algal species mentioned in this paper. The temperature data of surface water in San Francisco Bay used in this study were furnished the writer through the courtesy of Captain C. D. Washburn, Jr., of the Branch Hydrographic Office, U. S. Navy, San Francisco, to whom I am indeed grateful. Without the material aid extended by the Department of Zoology at the University of California, this study would have been impossible, and much credit is due to the University of Hawaii for extending many facilities necessary to bring this research to a successful conclusion.

To my wife, Elizabeth, I owe an immeasurable amount of gratitude for her constant encouragement and generous assistance both in the field and in the laboratory. Dr. D. C. Matthews, of the Department of Zoology at the University of Hawaii, and Mrs. Matthews gave generously of their time to assist in critically reviewing the manuscript.

TAXONOMY

Synonymy

Pachygrapsus crassipes Randall. 1839. Acad. Nat. Sci., Phila., Jour. 8: 127 (type locality, Sandwich Islands; this locality is probably erroneous; type in Mus. Phila. Acad. Nat. Sci.); de Man. 1890. Notes Leyden Mus., 12: 86, pl. 5, fig. 11; Rathbun. 1917. U. S. Natl. Mus., Bul. 97: 241, pl. 59.

Grapsus eydouxi Milne-Edwards. 1853. Ann. Sci. Nat., ser. 3, Zool., 20: 170 (type locality, Chile; this also is probably an erroneous locality record; type in Paris Mus.).

Leptograpsus gonagrus Milne-Edwards. 1853. Ann. Sci. Nat., ser. 3, Zool., 20: 173 (type locality unknown; type in Paris Mus.).

Stimpson (1857), Kingsley (1880), de Man (1890), Rathbun (1917), and Boone (1927) concur in the opinion that *Leptograpsus gonagrus* H. Milne-Edwards, for which the type locality is unknown, is identical with *P. crassipes* Randall. The meager description of *L. gonagrus* by Milne-Edwards (1853) agrees with the specific characters of *P. crassipes*. Furthermore, Milne-Edwards substituted the name *Leptograpsus* for *Pachygrapsus*. Stimpson (*op. cit.*) advanced several reasons for retaining the name *Pachygrapsus* for the group designated *Leptograpsus* by Milne-Edwards.

Kingsley (1880), Rathbun (1917), and Boone (1927) believe that *Grapsus eydouxi* Milne-Edwards is likewise synonymous with *P. crassipes* Randall. Here again it is obvious that the description of *G. eydouxi* as set forth by Milne-Edwards (1853) agrees with that of *P. crassipes*. It seems rather incongruous, however, that he should place two apparently similar specimens in different genera in the same revision. The type locality for *G. eydouxi* is cited as Chile. If this is correct, *G. eydouxi* is not synonymous with *P. crassipes* because the latter crab does not occur on the Latin American coast (see p. 138).

Systematic Position

P. crassipes is one of eleven species of a genus distributed in a nearly cosmopolitan manner. Its members inhabit both the Pacific and Atlantic coasts of America, the western coast of Africa, coasts bordering the Mediterranean, and the Indo-Pacific, and Central Pacific shores. Four genera of the family Grapsidae have been reported from the California coast; they may be readily distinguished from each other (see key in Schmitt, 1921: 269). The seven species of *Pachygrapsus* recorded from North and South America may be identified by the use of the key in Rathbun (1917: 241).

Description

Although a moderately complete, generalized, morphological description of *P. crassipes* is given by Rathbun (1917: 242), no information is made available by this or other authors with regard to sexual dimorphism. Measurements of the length and width of the carapace of several hundred crabs show that the males average larger than the females. The mean width of the carapace of adult males which ranged in size from 16.0 to 45.8 millimeters was found to be 36.8, with a standard deviation of 11.2. Similar measurements on adult females which ranged from 15.0 to 39.7 millimeters showed the mean width to be 30.9, with a standard deviation of 4.7. The mean length of the carapace of adult males was found to be 31.6 millimeters, with a standard deviation of 9.6. Similar measurements of females showed the mean length to be 26.4 millimeters, with a standard deviation of 3.9. These differences in size between the sexes do not become apparent until the crabs reach a carapace width of 22 millimeters (see Fig. 10), after which the carapace of female crabs becomes relatively narrower and shorter than that of male crabs of the same age and belonging to the same intermolt period. The usual brachyuran sexual dimorphism in the abdomen is apparent. Sexual differences in the chelipeds are pronounced, those of the male being approximately 8 per cent longer. The propodite and dactylopodite of this appendage exhibit the greatest difference; those of the males exceed those of the females by approximately 10 per cent.

Type Locality

The assertion by Randall (1839) that the type locality of *P. crassipes* is the Sandwich Islands (Hawaiian Islands), a region outside the normal geographic range of this species (Fig. 1), has made obligatory an investigation of this anomaly. Randall states that the type specimen of *P. crassipes* was collected on the shores of the Hawaiian Islands by Nuttall. However, frequent and thorough searches for decapod Crustacea in the Hawaiian Islands during the past century, in addition to recent explorations by myself, have failed to disclose this species.

Further, Randall states that the type specimen of *Metograpsus messor* (Forskål) (= *Pachygrapsus parallelus* Randall) was found on the coast of Oregon by Nuttall during the same voyage. It, in turn, has not been known to occur on the American coast, but it is common on the Hawaiian Islands. Inasmuch as the names are correctly affixed on the type specimens, Stimpson (1857) made a rather likely suggestion; namely, that the labels giving the collection localities of the two species in Nuttall's collection were in some way accidentally exchanged. Holmes (1900) also points out that several other species reported from the Pacific coast by Randall have not since come to light.

DISTRIBUTION

Geographical Distribution

The authenticated geographical range of *P. crassipes* extends along the western coast of North America from north latitude 45° (Newport, Oregon) to north latitude 24°20′ (Santa Margarita Island, Baja California), and along the coast of Japan and Korea from north latitude 34° to 37°.

A number of records outside the above localities had to be considered in an attempt to establish the authentic geographical range. For example, Rathbun (1917) cites Chile as a collection locality. Correspondence with Dr. C. E. Porter, an active carcinologist in Chile, has established the fact that *P. crassipes* does not exist along Latin American shores. Therefore, either *Grapsus eydouxi* (see Synonymy, p. 136) is not synonymous with *P. crassipes* or the type locality of the former is incorrect.

Rathbun (1902) also cites the Galapagos Islands as another locality of collection. The specimen upon which the record is based was taken at 12 fathoms, a depth in decided contrast to the well-known habits of the species elsewhere. This, together with evidence supplied by Garth (1946), indicates that *P. crassipes* is not a member of the Galapagan fauna and that the specimen catalogued from there, which I have seen and know to be *P. crassipes*, was in some manner mixed with specimens collected from the west coast of America on the same expedition.

P. crassipes is associated geographically with but one other congener, *P. transversus* (Gibbes), and with it only toward the southern boundary of its range on the east and west coasts of Baja California and the west coast of Mexico. Heretofore, the two species have been thought to overlap in the Galapagos and Cocos Islands. A great difference in size enables one to distinguish quickly between these two forms. The length of the carapace of a large specimen of *P. crassipes* is approximately 40 millimeters, the width approximately 44 millimeters. *P. transversus*, on the other hand, is only half as large; the length of a large specimen is about 15 millimeters, the width about 20 millimeters. The most striking diagnostic character is the width of the front, which in *P. crassipes* is half or almost half as wide as the carapace; whereas in *P. transversus* the front is distinctly more than half as wide as the carapace.

The geographic distribution of *P. crassipes* is completely disjunctive. The individuals on the coast of Japan are separated from those on the west coast of America by the wide expanse of the Pacific Ocean (Fig. 1). To account for this distributional phenomenon, it is necessary to assume that the migration between the two continents was somehow accomplished without leaving tangible evidence of the process. The physical characteristics of its habitat (p. 142) offer little assistance to the solution of the distributional pattern, largely because this species possesses a wide substrate tolerance and is somewhat eurythermal. Moreover, although rocky shore line is common along the coast of Korea and Japan, the animals there are restricted to a narrow band of latitude 2.5° to 3° in extent.

The isothermic pattern for surface water and air temperature at sea level during both summer and winter in Japan and America (see Schott, 1935) fits a wide latitudinal spread on the western coast of North America but is strongly

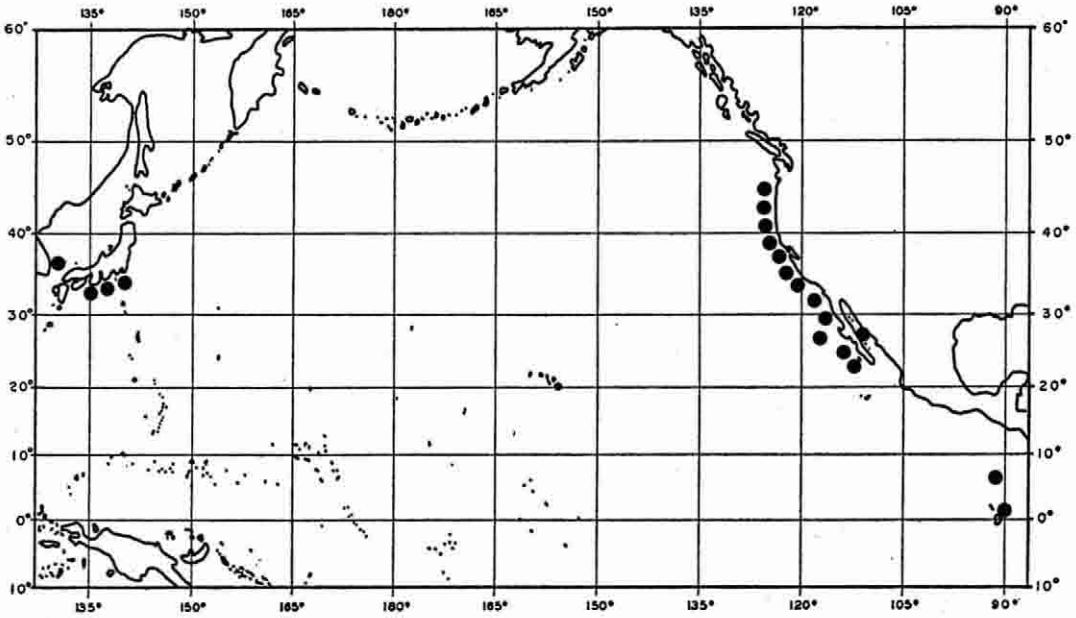


FIG. 1. A map of the Pacific area indicating the world distribution of *P. crassipes*. Each round spot represents a locality from which this species has been reported.

convergent in the region of Japan. This isothermic pattern seems to offer a distinct clue as to why the latitudinal distribution of this species is restricted in the Orient. However, more critical examination shows that the tolerable temperature range for this species as exhibited on the Pacific coast of America is almost nowhere fully occupied in the Oriental region.

That this species could, but does not, possess a greater latitudinal distribution in the Orient indicates that either (1) control of its distribution is accomplished by factors (food supply, parasites, etc.) which have not been taken into consideration because of insufficient knowledge of the Oriental region, or (2) the presence of this species in the Orient has been of relatively recent occurrence. The latter hypothesis seems unwarranted, however, for reasons cited below.

Extremely rapid invasions of new areas are known to have been accomplished by this and other species of Crustacea. Stebbing (1888, 1893, 1906), Alcock (1899, 1900), Fulton and Grant (1901), Chilton (1911), and Panning (1939) have recorded numerous observations of Crustacea which, by means of transoceanic shipping, have attained new frontiers. Some of these transportations have been successful, e.g., *Eriocheir japonicus* as described by Panning (1939). It is certain that at present, and for a long time past, the dispersal of *P. crassipes* over its geographical range could not have occurred by a littoral migration along the north Pacific shores, presumably because of the unfavorable temperatures. The low winter temperature along the Oregon coast probably delimits the northern extent of this species; other ecological requirements seem satisfactory farther northward. If a littoral migration of this type had taken place when the climate was temperate along the north Pacific shores, one would expect to find some manifestation of morphological change accompanying the long isolation of the populations. However, the American and Japanese types are apparently identical.

Although the currents in the Pacific are favorable for the transportation of pelagic fauna between American and Japanese coasts, it is highly improbable that this species was dis-

persed in this manner. The first crab stage, which is no longer free-swimming, occurs approximately 5 weeks after hatching. The time, therefore, is far too short for a successful ocean crossing by larvae. The possibility of the use of natural rafts as vehicles cannot be dismissed lightly in view of the habits and habitat of this form. However, both these hypotheses seem less plausible than the suggestion to follow.

Since *P. crassipes* was not mentioned in the faunal accounts of Japan until 1890, it is not unreasonable to speculate on the probability that marine traffic between the west coast of America and Japan has supplied the medium of dispersal. The extensive reproductive season of this species would insure the presence of a quantity of zoeae swarming in the harbors. These zoeae may easily have been taken into the ballast tanks of ships which were filled on the California coast and subsequently emptied in Japanese waters. Inasmuch as the ecological requirements of the niche are fulfilled in Japan, it seems feasible that the species would become established; in fact, a constant intermixing of this nature may explain the uniformity of the species in the two widely separated areas.

Habitat and Ecologic Niche

P. crassipes is a eurytopic species which ranges through the depositing shore and eroding shore subbiochores; consequently, it is necessary to designate the characteristics of the habitat in general, and to subdivide this general habitat into the three biotopes and fasciations which the writer considers most significant. Generally speaking, the habitat of this crab is that region of the strand extending from upper low (0.0 tide level) to highest high intertidal zone (6.0-foot tide level in the San Francisco Bay region) where there is a hard substrate containing crannies, crevices, or holes, free from loose stones, sand, or mud, and supporting a more or less luxuriant growth of ulvaceous or filamentous algae.

With respect to the vertical distribution on the strand, the present data show that this species may be located in crevices in the adtidal zone (at Pacific Grove, California) as low as the – 0.7-foot tide level. However, the individuals at this level were secluded in refuges at the base of nearly vertical rocky promontories which extend several feet out of the water at high tide. It is assumed that they had followed the receding water level, since the crevices they usually occupy are located in the intertidal zone higher up the rock. Such vertical migrations of a few feet are common, in contrast to a lack of extensive horizontal movements. Where no rocks protrude at high tide, the crabs are absent from crevices at the – 0.7-foot tide level, thus furnishing evidence for the preceding assumption. The greatest proportion of crabs are to be found in crevices and tide pools at the lower edge of the supratidal zone. Relatively fewer are found higher in the supratidal zone (from the +5.0- to the +8.0-foot tide level at Pacific Grove) and the area slightly above, except at night. Additional information on this phase of distribution is presented in the section on foods and feeding habits.

The first and most important biotope is characterized by large rock promontories. These rocks are generally continuous and unbroken by tide channels from points high on the shore to the low-tide level. Their multiplicity of crevices affords the crabs refuge from danger during the periods of the day in which activity is minimal. The greatest concentration of crabs is found in the crevices of these rocky coasts. Tide pools of varying depths are frequently encountered, all of which provide activity centers for the crabs. Much of the coast line in the region of central California is of this type; Plate 1, Figure 1, illustrates a typical rocky habitat at Pacific Grove, California.

Microscopic algal forms associated with this biotope at Pacific Grove consist in the main of the following types: around the edges of the tide pools and in damp crevices are found juvenile sporelings of some ulvaceous alga, several species of non-colonial diatoms, an abundant supply of *Oscillatoria* sp., a sparse supply

of *Lyngbya* (two species), and a sparse supply of *Cladophora* sp. It is the foregoing group of plants which form the greater part of the food consumed by *P. crassipes* in central California.

In addition to the minute algae the following macroscopic forms are significant in the life of this crab:

Ulva lactuca L.: This species is sparsely represented in the first biotope on the tops and sides of the rocks just below high-tide level; it is of less importance here than in the second biotope to be described.

Fucus furcatus Ag.: An abundant species which supplies this animal both cover and food.

Enteromorpha sp.: A common species which provides considerable food. Longer fronds furnish effective cover for small crabs (many of the small, recently molted individuals may be collected under this alga).

Grateloupia Setchelii Kylin and *Rhodoglossum affine* (Harv.) Kylin: Both species are common in high tide pools and are consistently used by the animals for food.

Endocladia muricata (Harv.) J. Ag.: This species grows on the rocks in and immediately below crevices near high-tide level. It is a relatively important source of food.

The algal forms listed below are, as a group, less important than the above types. Algal fronds broken from plants lower in the strand or from pelagic types may often be found floating in the high tide-pools; these floating pieces are often seized by the crabs and partially devoured; thus, they are important integers in the life equation of this animal.

Cryptopleura lobulifera (J. Ag.) Kylin: Found floating in tide pools at high-tide level.

Laminaria Sinclarii (Harv.) Farlow: Found floating in tide pools at high-tide level.

Macrocystis pyrifera (L.) C. A. Ag.: Found floating in tide pools at high-tide level.

Pelvetiopsis limitata (Setchell) Gardner: On rocks and in tide pools just below high-tide level.

Gelidium sp.: Growing in rock crevices at high-tide level.

Gigartina leptorhynchos J. Ag.: Growing in tide pools at high-tide level.

Iridophycus sp.: Growing on rocks just below high-tide level.

Egregia Menziesii (Turn.) Aresch.: Growing on rocks just below high-tide level.

Cladophora graminea Collins: Growing in crevices containing sand just below high-tide level.

Gastroclonium Coulteri (Harv.) Kylin: Growing on rocks just below high-tide level.

Agardhiella Coulteri (Harv.) Setchell: Growing on rocks just below high-tide level.

Corallina officinalis L.: Growing in tide pools just below high-tide level.

Gigartina Harveyana (Kuetz.) Setchell and Gardner: Growing on rocks in tide channels just above low-tide level.

Gigartina corymbifera (Kuetz.) J. Ag.: Growing on rocks in tide channels just below low-tide level.

Cryptopleura violacea (J. Ag.) Kylin: Growing on rocks in tide channels just above low-tide level.

The second and less common biotope is found along the outer coast, as well as along man-made shore lines which are met most commonly in estuaries and bays. This type is characterized by the presence of large, relatively stable boulders, which occupy an area of the strand coinciding with the intertidal range of this species. On the outer coast these boulders generally rest upon a solid substrate of smooth rock or upon other boulders. Along estuaries, e.g., the Oakland Estuary in the San Francisco Bay, granite boulders have been arranged two or three deep along the shore, extending from low- to high-tide level; very few project sufficiently high to be in a position comparable to the splash zone of the outer coast. At the upper limit of these boulders along the estuarine strand the terrain becomes flat, and the boulders gradually decrease in number and size. The crevices requisite for the existence of this species are formed by the contiguous surfaces of the boulders. The crab population in this habitat shows a progressive decrease from the large boulders placed low on the strand to the smaller ones farther shoreward. This gradient in population may be attributed to the fact that the boulders extending shoreward are smaller, stacked in a more shallow layer, and tend to be more deeply imbedded in mud or sand; such conditions manifestly reduce the number of available refuges. In these areas where environmental conditions for *P. crassipes* are met along a rocky embankment, shoreward of which occurs a narrow, relatively muddy tidal flat, the usual linear order of grapsoid habitation on the strand becomes inverted. In this terrain one frequently encounters both *Hemigrapsus nudus* Dana and *H. oregonensis* Dana farther shoreward than *P. crassipes;* whereas in the first biotope both these species frequent comparatively lower fasciations in the littoral zone than the subject of this study.

This invasion may be attributed jointly to the decreased number of suitable refuges for *P. crassipes* and the muddy nature of the substrate in the high, flat zone which is suitable habitat, especially for *H. oregonensis.*

The algal species contributing most to the general welfare of *P. crassipes* in this estuarine habitat is *Ulva lactuca,* whose short fronds or very young sporelings form the principal food for this crab. *Ulva* is abundant on the large boulders from middle high- to high-tide level; the plants become progressively smaller as the high-tide level is approached.

The third and least common biotope in which *P. crassipes* is found is the muddy shore of bays and estuaries. Along these, restricted to high-tide level, are numerous individuals which take refuge in small holes in the mud bank. Extended observations have furnished evidence that the holes are not dug by the crabs, but are excavated by wave action which has removed the loose mud and sand from the netted roots of a dense stand of pickleweed (*Salicornia ambigua* Michx.) which grows shoreward from high-tide level. The splash zone, here an area extending back on a slight incline from the bank, is covered by a dense growth of *Ulva lactuca* which grows on the hard mud between the stems of *Salicornia.* This growth of *Ulva,* the lone macroscopic algal species present, covers a flattened area extending approximately 5 feet back from the top of a bank on a level with the high-tide mark. The habitat described above is typical of portions of the shores of Bolinas Bay, Bodega Lagoon, and Elkhorn Slough (Pl. 1, Fig. 2).

The vertical section of the bank varies from 6 to 18 inches in height; the crest of the bank corresponds to the "upper high" intertidal zone, and the base is on a level with the "middle high" zone. Consequently, the vertical range of the crab habitat is restricted when compared with other types of terrain outlined above. From the base of the bank the intertidal zone consists of a down-sloping stretch of mud containing gravel and sand. At the ebb of a – 0.5-foot tide this slope averages approximately 25 feet in breadth, and a medium high tide completely submerges it. The receding tide serves to deposit on this slope a myriad of organisms killed by the extensive clam digging operations which occur at many points along these bays and estuaries. A wealth of animal food in addition to the abundant algal supply is thereby provided. *P. crassipes* has never been observed to venture more than 4 to 5 feet away from the refuge holes in the banks; hence it offers little, if any competition to *H. oregonensis,* which likewise occupies holes in the bank, but characteristically forages over the entire expanse of the submarine slope. The latter species accepts any available organic matter and seems to forage typically as a true scavenger.

P. crassipes may well be considered a eurytopic species because of its wide distribution along the entire width of the strand. The population is greatest at the typical high fasciation, and follows a decreasing gradient in abundance farther landward as well as farther seaward. In the first biotope mentioned, the habitat conditions consist of those deep crevices in or near tide pools at the high-tide level, with an abundant supply of filamentous or ulvaceous algae at hand. The habitat characteristic of the second biotope may be designated as those crevices under or between large boulders which ordinarily have a dense growth of *Ulva* or other minute forms of algae on their exposed surfaces. The topography characteristic of the third biotope consists of shallow holes in hard mud banks, immediately above which is an abundant supply of ulvaceous algae.

The primary topographic units described above apparently provide all the factors requisite for the welfare of the species: a hard substratum (rock or solid, packed mud), ample food which consists primarily of the more minute species of algae and secondarily of dead animal tissues, protection from wave action and predators by seclusion in crevices, and insurance against desiccation by close association with tide pools or damp crevices into which the sun's rays do not penetrate.

The trio of closely associated grapsoid crabs along the central California coast (*P. crassipes, H. nudus,* and *H. oregonensis*) exhibit distinct preferences for certain types of substrate, notwithstanding the fact that the habitats preferred overlap to a certain minor degree. In order to ascertain more specifically the underlying causes for this habitat preference, an analysis of the preferred physical features of the environment of each species was made, after which certain pertinent structural, physiological, and behavioristic comparisons among the crabs were made. It was found that *H. oregonensis* prefers a muddy, silty substrate; *H. nudus* is found more commonly on a sandy or gravelly bottom; and, as indicated above, *P. crassipes* shows a preference for the hard, non-silty substrate. A clue to this distributive pattern may possibly be found in a study of the structures concerned with external respiration, inasmuch as it is necessary that a constant supply of clean water be carried through the branchial chamber. An examination of the abundance and position of setae, both in the vicinity of the incurrent openings to the branchial chamber and on the mastigobranch of the third maxilliped, was made.

A thick mat of very fine setae on the branchiostegite immediately above the coxae of the pereiopods is easily observed in *H. oregonensis.* The dorsal side of each coxa likewise bears a thick tuft, which, with the setae of the branchiostegite, forms a fine strainer covering the incurrent openings to the branchial chamber. Functional evidence for this setal sieve is apparent since a heavy deposit of silt covers the structure. The mastigobranch of the third maxilliped is exceedingly plumose, and serves to sweep the gill surfaces free of silt which does filter through the incurrent sieve.

The setae on the branchiostegite and pereiopodal coxae of *H. nudus,* although comparatively fewer in number, are far heavier than those of the preceding species. They arise in clusters of three and four on the branchiostegite and project ventrolaterally; those near the ventral border of the branchiostegite extend out to enmesh with those which originate on the base of the coxae. The stiff nature of these setae seems an adaptation for withholding large particles such as sand grains. The setae are heaviest on the ventral border of the branchiostegite above coxae 3, 4, and 5; those setae farther cephalad are less rigid, though more numerous. The mastigobranch of the third maxilliped is heavily plumose.

P. crassipes, on the other hand, exhibits fewer and finer setae. The branchiostegite, with the exception of the ventral border, is virtually devoid of setae. Those setae located on the ventral border of the branchiostegite enmesh with the relatively sparse, fine coxal setae to cover the opening to the branchial chamber. The mastigobranch of the third maxilliped has comparatively fewer setae than the two species previously described.

It is evident that these morphological differences in the rigidness and abundance of setae participate in establishing the character of the environment selected. The fine, dense mat of setae covering the incurrent channels of the branchial chamber in *H. oregonensis* is well adapted for straining out particles of a silt-like nature. Therefore, among other contributing factors, this structural adaptation enables this species to subsist on the soft, muddy banks of estuaries where it is especially common, and a habitat wherein the remaining two crabs under discussion cannot become established. *H. oregonensis* is rarely found associated with *P. crassipes* (except in the third biotope mentioned) probably because the former species cannot withstand the extended periods of desiccation which the latter type undergoes in its position high in the intertidal zone. However, in those estuaries wherein the fasciation of *P. crassipes* is lower than the highest tide level, and where sufficient cover is available to maintain relatively moist refuges, *H. oregonensis* does become a competitor for places of refuge; but, because of the diverse feeding habits the two species show little interspecific competition for subsistence. Associations of this type are to a

certain extent competitive in that the maximum number of each species present is probably not as high as it would be if only one species were present. It seems to be essentially an ecological compromise in which both species suffer quantitatively in the struggle for subsistence—further evidence of the great halobiotic pressure of the strand.

The rigid, clumped setae of *H. nudus* seem well adapted to withhold large grains of sand; an examination of the setae substantiates this assumption. It is apparent that the sparse but heavy setae are ineffective in straining out suspended silt; consequently, if the animals were placed on a muddy substratum respiratory difficulties would undoubtedly occur. This species and *H. oregonensis* are, therefore, only infrequently found associated. Where a close association exists, the substratum will normally be transitional between sand and silt. Both species in such an association are doubtlessly near the frontiers of their respective tolerances. *H. nudus* is often found associated with *P. crassipes* where the latter occupies a position relatively low in the intertidal zone. However, at the high-tide level where *P. crassipes* is most abundant, very few individuals of *H. nudus* are found. Underlying causes for the virtual absence of *H. nudus* from areas with comparatively long exposures to air are obscure. No significant difference between the abilities of the two species to withstand desiccation was found. However, a clue to the inherent preferential differences with respect to habitat may be gained from the hydrotactic responses exhibited by each type.

P. crassipes is negatively hydrotactic; whereas, *H. nudus* and *H. oregonensis* are positively hydrotactic. This fact may readily be demonstrated by placing representatives of the three species in an aquarium which is tilted to provide deep water at one end and a dry area at the opposite end. The crabs will move to their preferred stations immediately; the latter two species submerge in the deep end, and the former species takes a position at the dry end. This behavior pattern of *P. crassipes* was utilized in the laboratory where the aquaria were tilted to simulate tide-pool conditions—deep water at one end and none at the other. The crabs spent most of each day at the shallow or dry end. Those reared in large tanks containing projecting rocks were observed upon the rocks the greater part of the time until they were disturbed, in which case they would dart underneath the rocks. This reaction to disturbance is typical of their normal littoral life, which will be discussed later. This negative hydrotactic response of *P. crassipes* is a prominent factor underlying its success, because this species alone, among littoral crabs, wanders onto the rocks high above the water to reach the uncontested food supply found there.

Preliminary experiments designed to test differences in the ability of these three local shore crabs to withstand desiccation were performed as follows: Representatives of each species of equivalent sizes in stage C_4 (see section on Intermolt Cycle, p. 146) were deposited in individual battery jars and placed in the same room to insure comparable external environmental conditions. Observations were then made at 15-minute intervals from 4:00 A.M. to 10:00 P.M. The interval of time which elapsed between the initiation of the experiment and the subsequent death of each animal was recorded.

It was found that *H. oregonensis* possessed much less ability to withstand desiccation than either *H. nudus* or *P. crassipes.* All individuals of *H. oregonensis* were moribund in 6 hours and all representatives of this group succumbed in 10 hours. None of the specimens of *H. nudus* and *P. crassipes* was moribund until 13 hours had elapsed, most of them lasting for a minimum of 18 hours. All were dead in 24 hours. No differences in tolerance to desiccation were apparent between *P. crassipes* and *H. nudus.*

A second experiment along similar lines was performed to test further the relative abilities of *P. crassipes* and *H. nudus* to withstand desiccation. This experiment was performed at the

TABLE 1

A COMPARATIVE SUMMARY OF THE NUMBER OF GILLS, VOLUME OF GILLS IN RELATION TO BODY VOLUME, AND HABITATS OF SELECTED LITTORAL BRACHYURANS ON THE COAST OF CENTRAL CALIFORNIA.

SPECIES	NUMBER OF SPECIMENS TESTED	NUMBER OF GILLS	PERCENTAGE OF GILL VOLUME TO BODY VOLUME		HABITAT
			Range	Mean	
Cancer antennarius	4	18	4.9–5.1	5.0	Low-tide zone and below; crevice dweller
Cancer magister	1	18	.....	4.4	Below low-tide mark; sandy substrate
Pugettia productus	4	18	3.1–4.0	3.72	On algae in tidal zone and off shore
Hemigrapsus nudus	3	16	2.7–2.8	2.77	Rockweed belt; sand below rocks
Hemigrapsus oregonensis	2	16	2.3–2.5	2.4	Tidal zone; muddy shores
Pachygrapsus crassipes	5	18	2.3–2.5	2.36	High-tide mark and above; rock crevices

seashore where normal environmental conditions prevailed. Ten specimens of *P. crassipes* and 12 specimens of *H. nudus*, all in stage C_4, were collected at Pacific Grove and placed in dry aquaria. The aquaria were concealed high on the rocks under a large boulder which excluded the direct rays of the sun. Observations were made at 15-minute intervals from 4:00 A.M. to 10:00 P.M.

The results of these tests were comparable with those obtained in the laboratory, except that death did not ensue as rapidly.

Under these seashore conditions, crabs of a size similar to those utilized in the laboratory lived approximately twice as long. A direct relationship between the size of the crab and the tolerance to desiccation was found; the smaller crabs became inactive and died sooner than the larger ones. Crabs of both species having a carapace width of approximately 40 millimeters lived about 48 hours. One specimen of *H. nudus* having a carapace width of 57 millimeters lived 70 hours. This apparent relationship between tolerance to desiccation and size seems to explain, in part at least, why smaller crabs of both species are invariably found in the most moist area of the habitat. These data demonstrate that the littoral horizon selected by each of the species concerned is not determined by its ability to withstand long periods of desiccation.

It is highly probable that some physical as well as physiological changes would occur in the respiratory mechanism of a crab which remained exposed to air for relatively extended periods. Further, this change should be correlated with the amount of exposure endured; therefore, a proportionate decrease in gill volume and surface to reduce desiccation would seem a reasonable supposition in view of the fact that ability to resist desiccation is generally dependent upon the surface area of external membranes. Pearse (1929*a*) has shown that as crabs become adjusted to a terrestrial life there is a gradual reduction in the number and volume of the gills. In order to ascertain the status of the gill-volume–body-volume ratio of *P. crassipes* in contrast to other Brachyura, a series of crabs was collected from habitats ranging from below low-tide level to above high-tide level.

The proportionate volume of the gills compared to the volume of the body was secured in the following manner: The crabs were hardened 24 hours in 1 per cent chromic acid and subsequently rinsed with tap water; pereiopods were removed at the fracture plane; the carapace was removed, and the gills were cut

free from their attachments; all parts were placed on blotting paper and allowed to drain for 5 minutes; the gills were then dropped into one graduate partially filled with water, and the remaining body parts into another graduate similarly filled; the volume was recorded as the difference in the column of water. The results are summarized in Table 1.

Unfortunately, crabs more highly adapted to a semi-terrestrial existence than *P. crassipes* were not available for this study; consequently, information was secured from statements concerning gill reduction in the near-terrestrial types made by Pearse (1929*a*). He has shown that some fiddler crabs (*Uca minax, U. pugnax,* and *U. pugilator*) have but 12 gills. Therefore, with the exception of *P. crassipes,* it may be assumed that in general crabs adapted to lengthy exposures to the air will have the gill number reduced. It follows that a reduction in the number and volume of gills is undoubtedly a critical factor in the selection of a habitat; i.e., *H. nudus* and *H. oregonensis* can withstand relatively long periods of desiccation because of a gill reduction, and consequently are found in the "middle high" intertidal zone, where they are exposed for many hours each day. *P. crassipes,* on the other hand, presents an enigma in that the usual number of gills (18) for strictly aquatic forms is not altered; however, the total volume of the gills in relation to the total volume of the body is the least of any of the animals examined; and the anterior arthrobranch of the second thoracic segment, the gill which is lost in both species of *Hemigrapsus,* is minute. Apparently, evolution with regard to the gills in *P. crassipes* has tended toward the reduction in size of all gills in lieu of reduction in number. The proportional percentage of gill volume to body volume in this species is somewhat less than in either species of *Hemigrapsus,* but seems inadequate to account for the tolerance of the former type to a drier environment. The slight difference between the gill-volume–body-volume relationship in the three grapsoid types corresponds with their similarity in resistance to desiccation. In fact, in the Puget Sound area where *P. crassipes* does not occur, *H. nudus* apparently ranges in the tidal horizon which would normally contain *P. crassipes*; however, the individuals of the former species at this higher elevation are smaller than those within the optimal environmental frontiers for the species (Ricketts and Calvin, 1939).

Sex Ratio

Sexual records from collected specimens were kept for 10 months of the year, not only to ascertain the relative numbers of the sexes, but to secure information on the supposed tendency of ovigerous females to sequester themselves. Virtually all the specimens were collected at night with the aid of a flashlight; hence no sexual discrimination occurred while collecting. A total of 2,224 animals was collected, of which number 1,141 were males and 1,085 were females. The nearly even sexual distribution (males exceed females by approximately 3 per cent), together with the fact that the females equal or exceed the males during 3 widely separated months, appears to indicate that monthly inequalities in sex ratio are insignificant. Furthermore, during August, when 1,264 crabs were collected at random, the sex ratio was virtually even, indicating that the ovigerous females at the height of the breeding season (28 per cent of all females collected were ovigerous) do not exhibit sequestering habits; indeed, the proportionate number of females actually increased during the breeding season.

INTERMOLT CYCLE

The phenomenon of molting and filling of the haemocoelic spaces by imbibition of water has been considered by most workers to be a recurring event in the life of Crustacea with the intervening period between actual molts a more or less static one. However, the profound transformations occurring within the Crustacea from the conclusion of one molt to the termination of the one following are a continuous series.

Since *P. crassipes* is available and easily collected along most of the west coast of the United States, and since it readily adapts itself to laboratory confinement, it will doubtless become an important experimental animal. Consequently, it would be advantageous in controlled experimental studies to know the precise intermolt condition of the animals employed. The chief objective in this study of the intermolt cycle was to ascertain the internal changes and to select some external morphological feature which would enable the worker to identify the internal or physiological condition.

It is important to note that the changes during the intermolt cycle from its initiation to its termination do not differ with the size and age of the crab. The crab increases progressively in age throughout the intermolt cycle, and its completion is manifest by exuviation which is the result of an increase in size, but the physiological level at the onset of the following intermolt cycle is exactly comparable to the like part of the preceding cycle. These transformations, largely concealed during the intermolt cycle, are exhibited after ecdysis. Therefore, we may define the intermolt cycle as a series of transformations occurring during the period between the molts, not including the preceding or the impending molt.

The literature relating to the intermolt cycle contains many expressions which designate various externally recognizable physiological conditions, such as "soft crab," "hard crab," "turgid crab," and "limp crab." All of these terms refer more or less directly to the amount of water or haemocoelic fluid contained in the tissues and haemocoelic spaces. Olmstead and Baumberger (1923) were the first investigators to analyze scientifically these intermolt conditions.

Early workers recognized a series of physiological changes for one or more periods within the intermolt cycle, but none considered the entire cycle representative of a continuous succession of events. The search for knowledge relative to the formation of the integument led several investigators to discover isolated anatomical and physiological phenomena with regard to the intermolt cycle. The most notable of these findings were (1) the discovery of the accumulation of calcareous reserves on the walls of the stomach; (2) the formation of setae; (3) the secretion of chitin. All of these phenomena were detected by Braun in 1875 while studying the macruran, *Astacus fluviatilis*. Unfortunately, they were discovered in studies confined to stages immediately preceding the molt and no attention was directed to earlier transformation; hence he recognized no seriation. The meticulous investigations of Vitzou (1882), accomplished during observations on the histogenesis of the brachyuran integument, did not impress upon him that a seriation occurred during endysis. Paul and Sharp (1916) found the initial clue to seriation through bioassays of the ratio of hepatopancreas weight to body weight in the crab, *Cancer pagurus*. Elmhirst (1923) employed the traditional "premolt," "post-molt," and "intermolt" intervals. Later, Yonge (1932) discovered a series of stadia correlated with the amount of reserve calcium in the stomach walls of the lobster, *Homarus gammarus*, but this character is not available for use in studies on Brachyura, because, with the exception of certain land crabs (Stebbing, 1893), nothing equivalent has been discovered in the Brachyura. Most of the seriation described prior to the studies of Olmstead and Baumberger (1923, 1928) is founded upon the interval of time elapsing after ecdysis. It is at once apparent that this method is restricted in utility because (1) it is inadequate for comparative studies between species in view of the established interspecific differences with respect to the time lapse during the intermolt interval; (2) it is inapplicable for intraspecific comparisons because the intermolt interval varies directly with age; (3) crabs reared under dissimilar environmental conditions show inconsistent intermolt intervals.

Olmstead and Baumberger, recognizing the need for a more accurate estimation of the

intermolt condition of crabs utilized for experimental purposes, subdivided the total cycle into six stages: (1) "newly molted," (2) "soft," (3) "paper shell," (4) "hard," (5) "pillans," and (6) "about to molt." Each term describes the character of the integument which in turn is affected by the amount of water in the tissues and haemocoelic spaces and the impregnation of the integument with calcareous materials. Although this system provides a rapid means of grouping crabs, it possesses certain disadvantages. For example, the stage "pillans," the duration of which is 3 or 4 days at the maximum in *P. crassipes,* is confused with the latter part of the period "hard" and the early part of the period "about to molt." Furthermore, the stage "hard" includes several easily distinguishable stadia which are of considerable importance in the cycle.

Recently, the solution to the problem of securing a near universal method for both inter- and intraspecific comparisons during the intermolt period was proffered by Drach (1939), and it is upon his studies on *Maia squinado* Herbst, *Cancer pagurus* Linné, and *Carcinides maenas* (Linné) that this study of the intermolt cycle of *P. crassipes* is based.

Drach sought to establish a series of morphologically determinable "stadia" throughout the intermolt cycle in order to construct a standardized key to the changes which occur. Several criteria for the establishment of these stadia were selected: (1) each stadium should correspond to a definite internal transformation; (2) the key characters for the extremes of any stadium must be easily recognizable, differing considerably from those of the stadium preceding or following; (3) a sufficient number of stages should be established so that only a small fraction of the animals examined falls into any one classification; (4) these stadia must be so established that all animals collected may be successfully and rapidly classified. This approach to the problem seems valid because it considers the continuous activity throughout the entire intermolt cycle and is directed away from former designations which imply stages of both morphologic and physiologic inactivity. The advantages of this system may be briefly summarized: (1) it is usable for both wild and captive specimens; (2) it is valid for comparison between different intraspecific age classes; (3) it is adapted for comparative interspecific use because of the high degree of uniformity between the higher Crustacea with regard to endysis.

The present study supplements the information contributed by Drach for the cancroid and oxyrhynchoid types by extending the knowledge of the transformations occurring throughout the intermolt cycle to a third cosmopolitan group, the grapsoid type.

The classification presented here for *P. crassipes* is a modification of that set forth by Drach. Throughout the classification of the cycle, external morphological signs have been employed where possible, and each has been checked by utilizing some character concerned in the genesis of the integument. The hardening of the exoskeleton is diagnostically accurate, but the major portion of the cycle occurs during the time in which the exoskeleton is hard; hence, other indicative characters must be employed. The precocious development of the spines of the new integument furnishes the diagnostic character utilized after the old integument becomes totally rigid. To facilitate the interspecific comparative aspect, Drach's method of designating the various periods and stages is adhered to.

The cycle is composed of four major divisions designated A, B, C, and D. Each major period is subdivided into stages with numerical indices corresponding to the order of succession. A major period, during which minor but distinct transformations occur, frequently will have correspondingly more stage indices than a major period during which but few transformations occur. For example, A, a very brief period, exhibits two distinct integumental transformations designated as stages A_1 and A_2; while C, a relatively long period, exhibits four major integumental transformations, C_1, C_2, C_3, and C_4. The major periods are equivalent in all species,

but the supplementary stages which are diagnosed in the initial portion of the intermolt cycle by differential sclerotization of the integument vary with the shape of the carapace of the crabs concerned. The curvature and thickness of the carapace differ for each species, hence, each must be studied individually to determine the adaptability for any standardized series of intermolt stages. This procedure was followed in the present study; the sequence of sclerotization is shown in Table 2. It was noted that differences between these data and those presented by Drach (1939) for *M. squinado* were slight; consequently only slight modification was necessary to adjust the criteria involved in designating comparable stadia. This succession of rigidity in the various areas of the integument was found to be constant regardless of the size of the animal or the temperature of the water.

TABLE 2

SUMMARY OF POST-EXUVIAL SCLEROTIZATION AND LOSS OF FLEXIBILITY IN VARIOUS INTEGUMENTAL REGIONS OF A SPECIMEN OF *P. crassipes* WITH A CARAPACE BREADTH OF 28.5 MILLIMETERS. SIGNS: ++, INTEGUMENT COMPLETELY SOFT; +, INTEGUMENT PARTIALLY RIGID BUT EASILY DEPRESSED; —, INTEGUMENT COMPLETELY RIGID.

DAYS AFTER MOLT	CARAPACE						THORACIC STERNITES	CARPUS AND PROPODUS OF CHELAE	MERUS AND CARPUS OF WALKING LEGS	STAGE
	Proto-gastric Area	Meso- and Urogastric Area	Anterior Branchial Area	Posterior Branchial Area	Branchio-stegites	Cardiac Area				
1	++	++	++	++	++	++	++	++	++	A_1
2	+	++	++	++	++	++	++	++	++	A_2
3	+	++	++	++	++	++	++	++	++	A_2
4	—	++	++	++	++	++	++	+	++	A_2
5	—	++	++	++	++	++	++	+	++	A_2
6	—	+	+	++	++	++	++	+	++	B_1
7	—	+	+	++	++	++	++	+	++	B_1
8	—	+	+	++	++	++	++	+	++	B_1
9	—	+	+	++	++	++	+	+	++	B_1
10	—	+	+	++	++	++	+	—	++	B_2
11	—	+	+	++	++	++	+	—	++	B_2
12	—	+	+	++	++	++	+	—	++	B_2
13	—	—	+	+	++	++	+	—	++	C_1
14	—	—	—	+	+	+	+	—	++	C_1
15	—	—	—	+	+	+	+	—	++	C_1
16	—	—	—	+	+	+	—	—	++	C_1
17	—	—	—	+	+	+	—	—	+	C_1
18	—	—	—	—	+	+	—	—	+	C_2
19	—	—	—	—	+	+	—	—	+	C_2
20	—	—	—	—	+	+	—	—	+	C_2
21	—	—	—	—	+	+	—	—	+	C_2
22	—	—	—	—	+	+	—	—	+	C_2
23	—	—	—	—	+	+	—	—	+	C_2
24	—	—	—	—	+	+	—	—	+	C_2
25	—	—	—	—	+	+	—	—	+	C_2
26	—	—	—	—	+	+	—	—	+	C_2
27	—	—	—	—	+	+	—	—	+	C_2
28	—	—	—	—	+	+	—	—	+	C_2
29	—	—	—	—	+	+	—	—	+	C_2
30	—	—	—	—	+	+	—	—	+	C_2
31	—	—	—	—	+	+	—	—	+	C_2
32	—	—	—	—	+	+	—	—	+	C_2
33	—	—	—	—	+	+	—	—	+	C_2
34	—	—	—	—	—	—	—	—	—	C_3

Prior to a consideration of the diagnostic characters for each intermolt stage, a brief summary of the morphologic pattern of the integument is presented, since a knowledge of integumentation is necessary in order to implement definitions of stadia. The integumentary pattern was studied and accurately described as early as 1860 (Williamson), but we owe our present extensive knowledge of its histological composition to the work of Vitzou (1882). The integumentary strata are described briefly, beginning with the outer stratum and progressing inward. The laminar association of these strata may be observed in Figure 5.

1. A thin layer without definite morphologic structure (improperly designated cuticle), which should be termed epicuticle to be consistent with the corresponding formation in insects (Wigglesworth, 1933).
2. A series of parallel strata, unequally calcified, occasionally pigmented, which constitutes the pigmented layer.
3. A series of parallel strata, greatly calcified, generally devoid of pigment, thicker than the pigmented layer, and providing from three-fourths to four-fifths of the entire integument.
4. An internal layer consisting of a very thin lamella, which is densely chitinized but non-pigmented, and known as the membranous layer.

It has been known since the work of Vitzou (1882) that the epicuticle and pigmented layer are secreted by the epithelium before the molt and, therefore, underly the old integument; whereas, the principal and membranous strata are not secreted until after ecdysis.

The time intervals indicated in the following description of intermolt stadia are always the result of the function of several integrating factors. Important among these are the size of the individuals, the temperature of the water, and the adequacy of the food supply. The writer is acutely aware of the misconceptions stemming from data derived from captive animals; however, the variable factors in the environment were held to a minimum wherever possible. For example, the food supply, which in nature is abundant, was completely adequate in the laboratory insofar as could be ascertained; the mean daily temperature of the laboratory water varied from 15.2° C. in mid-April to 16.3° C. in June. The eight animals employed in this study ranged in size from 22.2 to 37.4 millimeters in carapace breadth. Differences in the intermolt interval ranged from 50 days for a crab 22.2 millimeters in width to 77 days for a crab 34.4 millimeters in width; the mean interval was 68 days. The above-mentioned intervals are somewhat longer than those occurring in nature for similar sized crabs. For this reason, the proportional percentage interval of each stage in relation to the entire intermolt interval is utilized. Although slight errors may occur in case of differential prolongation of certain stages in captive animals, the presentation utilized seems adequate for all practical purposes.

Period A. Duration: 1½ to 3 days; 4.0 per cent of the total interval. This is the period which immediately follows the molt. The carapace is completely soft and will depress at the slightest pressure of a finger. This period is subdivided into two stages:

Stage A_1. Duration: 8 to 12 hours; 1.5 per cent of total interval. During these early post-molt hours the integument has the consistency of a soft membrane. Movement is possible, but the animal moves only when disturbed and never elevates the body above the substrate. The color is brilliant in contrast to the pre-molt crab. Water is still being absorbed; weight and size are therefore indeterminate (Fig. 6). The turgidity of the gastric area, due perhaps to the filling of the stomach with water during imbibition, may be felt by passing the finger over this area of the carapace.

Stage A_2. Duration: 1 to 2 days; 2.5 per cent of the total interval. The carapace now has

a parchment-like consistency. The crab can elevate the body upon its legs and move with considerable agility. Water absorption has terminated and the weight is virtually constant henceforth. The color of the carapace is similar to A_1. No food is ingested as yet.

Period B. Duration: 4 to 6 days; 8.0 per cent of the total interval. The carapace is somewhat rigid, although deformable everywhere save in the protogastric area. The meso- and urogastric areas, together with the branchial areas, are somewhat rigid; the remaining regions, including the branchiostegites and sternal areas, remain plastic. The appendages are flexible and may be bent without breaking. Feeding is resumed by the larger crabs on the sixth day following the molt. This period is likewise divisible into two stages, depending upon the degree of rigidity of the chelae:

Stage B_1. Duration: 1½ to 3 days; 3.0 per cent of the total interval. The integument of the merus and propodus of the chela is relatively supple; it may be depressed without breaking. Most of the animals begin to take food during this stage.

Stage B_2. Duration: 2½ to 4 days; 5.0 per cent of the total interval. The integument of the merus and propodus now resists pressure; if great pressure is applied it will break.

Period C. Duration: 32 to 50 days; 67.0 per cent of the total interval. This period, the most extensive of the cycle, is initiated when the integumental areas become rigid, although some, exhibiting less convexity, may retain their plasticity throughout the first two stages of this period. Complete sclerotization is achieved by the onset of Stage C_3, making it mandatory that other diagnostic criteria for integumentation be employed beyond this point. This period contains four stages with a fifth stage a likelihood:

Stage C_1. Duration: 4½ to 5 days; 8.0 per cent of the total interval. Except for some elasticity in the anterior and posterior branchial areas together with the concave intestinal region, the carapace is completely rigid. The branchiostegites and sternites are still flexible, as are the carpus and merus of the ambulatory legs which may be bent in the flattened direction. The broad sides of the pereiopods may be squeezed together very easily.

Stage C_2. Duration: 7 to 10 days; 14.0 per cent of the total interval. With the exception of the intestinal area the carapace is entirely rigid. The branchiostegites, sternites, and ambulatory legs are less flexible but have not attained rigidity. It is rather difficult to distinguish between stages C_1 and C_2, inasmuch as these differences are a matter of degree. The recognition of each stage must be gained through experience.

Stage C_3. Duration: 7½ to 11 days; 15.0 per cent of the total interval. At the initiation of this stage the entire exoskeleton becomes rigid, making it easily distinguishable from Stage C_2, and the internal membranous layer has not yet been formed, thereby differentiating this stage from Stage C_4. At the termination of Stage C_2 the principal layer is completely synthesized, whereas the membranous layer becomes totally synthesized at the termination of Stage C_3. Therefore, the four integumental strata are complete at the onset of Stage C_4.

Stage C_4. Duration: 15 to 22 days; 30.0 per cent of the total interval. This is the most extensive stage of the cycle and is primarily characterized by the completion of the integumentary skeleton. The internal membranous layer, when present in its early stages of genesis, is not closely adherent to the more external principal layer synthesized previously. By cracking a portion of the carapace and cautiously elevating it, the shiny membranous layer is seen to overlie the epidermis. The distinction between Stages C_3 and C_4 is perhaps the sharpest between any two successive stages. For rapid diagnosis the following procedure has been

found to be more useful and more easily accomplished than chipping away the upper layers of the carapace: With the forceps, grasp one of the dactyls about midway of its length and break it by bending it first to one side and then to the other. After breaking, exert an outward tug in an attempt to withdraw the broken distal half from the proximal portion. The withdrawn portion of the dactyl consists of the three upper strata; the fourth layer (membranous layer), if present, will remain attached to the proximal half of the dactyl because it is not closely adherent to the three upper strata now withdrawn. The sac formed by the internal membranous layer retains the form of the removed dactyl. Caution should be exercised in the operation to avoid destroying the membranous layer. Stage C_4 is verified if the sac is present; if it appears absent, the stage is either C_3 or C_4T.

Stage C_4T. Duration: From Stage C_4 until the death of the crab. In this stage the internal membranous layer has become closely adherent to the principal layer and is not recognizable except upon histological examination.

This stage is common in most of the genera of larger Brachyura in which ecdysis occurs until the attainment of a certain maximum size; growth, therefore, ceases at this point. Its occurrence in *P. crassipes* seems substantiated by the evidence presented herewith. MacGinitie (1937) described a specimen covered with barnacles and even small *Mytilus edulis*. He omits size data, but from a knowledge of the duration of the early stages of the intermolt cycle this animal was probably in the C_4T stage. On August 5, 1940, three large males of *P. crassipes* (44.2, 47.2, and 47.8 millimeters in carapace breadth) were collected; each supported one specimen of *Balanus glandula* upon its carapace. One of the barnacles had a diameter of ¼ inch and the others were smaller. All three crabs were apparently in the C_4T stage. Moreover, a large male in the C_4 stage (width, 47.6 millimeters) was collected on August 15, 1940. Nearly 8 months later this crab was still in the C_4 stage with no evident signs of an impending molt. In field collections only one male over 44 millimeters in width was found in a stage later than C_4, but many were designated as C_4; likewise, no females over 40.0 millimeters in breadth were in a stage later than C_4. The evidence would seem to insure the validity of this stage, but so few crabs are collected near the maximum size that this stage must be generally uncommon and most crabs apparently die or are destroyed by predators, etc., before reaching a maximum size.

Period D. Duration: 10 to 16 days; 21.0 per cent of the total interval. During this period the integument undergoes a series of transformations preparatory to the impending molt, during the course of which the future spines are formed by the secretion of the epicuticular and pigmented layers of the new, developing integument. The termination of this period is marked by resorption of the lime salts of the integument in both localized and generalized areas. At the onset of the period a diminution of activity, which is accentuated as ecdysis approaches, is apparent. There are four easily identified stages in this period:

Stage D_1. Duration: 3½ to 6 days; 8.0 per cent of the total interval. This stage is marked by the formation of spines which are secreted several days before the initial chitinous stratum of the pigmented layer is deposited. When the dactyl is broken and examined, soft spines which push out the internal membranous layer overlying them can be observed. It is necessary to manipulate the membranous sac to bring the spines into view, inasmuch as their extreme softness causes them to be closely appressed to the surface of the sac. This character is the only clear-cut distinction between C_4 and

D_1, there being no important changes in the old integument. However, toward the latter portion of this stage gelatinization of the membranous layer is initiated. This may be easily demonstrated by chipping off a segment of the carapace. The broken piece will become freed very easily and will reveal the gelatinous layer below. Muscular insertion on the old integument is not impaired since no great diminution in muscular activity is yet apparent.

Stage D_2. Duration: 3½ to 6 days; 8.0 per cent of the total interval. This stage is characterized by secretion of part of the pigmented layer. Diagnosis is based upon the chitinization of the spines, which are hard in this stage. When the dactyl is exsheathed the new dactyl appears similar to the old removed portion, as though the old integument were a glove covering the new.

Stage D_3. Duration: 1½ to 3½ days; 4.0 per cent of the total interval. Resorption has now progressed sufficiently far to be recognized. Slight pressure on the epimeral line will result in its splitting along its entire length. The membranous layer is completely gelatinous, and resorption is virtually completed in all parts of the exoskeleton. The activity of the crab is much reduced.

Stage D_4. Duration: 12 to 15 hours; 1.0 per cent of the total interval. This abbreviated stage immediately precedes exuviation. Resorption is now complete, and the epimeral line splits along its entire length. The activity of the crab entirely ceases because the muscles are now inserted on the supple, new integument. The carapace is elevated posteriad and exuviation ensues.

In an effort to test the validity of the identification of the various intermolt stages, a comparison was made between the intermolt condition of animals collected in the field and the proportional percentage of time represented by the individual stages of the entire cycle as ascertained from captive specimens. A field examination to ascertain the intermolt stage of 574 individuals was made in 4 days during August, 1940. Frequencies of crabs within the various intermolt stages, together with the proportional interval for any given intermolt stages as determined by laboratory methods, are indicated in Figure 2. A marked correlation between field and laboratory data is apparent, thus serving to confirm in part the criteria for the divisional diagnoses of the intermolt cycle set forth above.

Several phenomena which normally would be discussed in other sections of this paper are briefly considered at this time because of their direct association with various intermolt stages. Throughout the examination of the several hundred specimens mentioned in the paragraph above, it was noted that ovigerous females constantly fell into stages C_3 and C_4. The data indicate that of a total of 80 ovigerous females, 23 were classified as stage C_3, 55 were placed

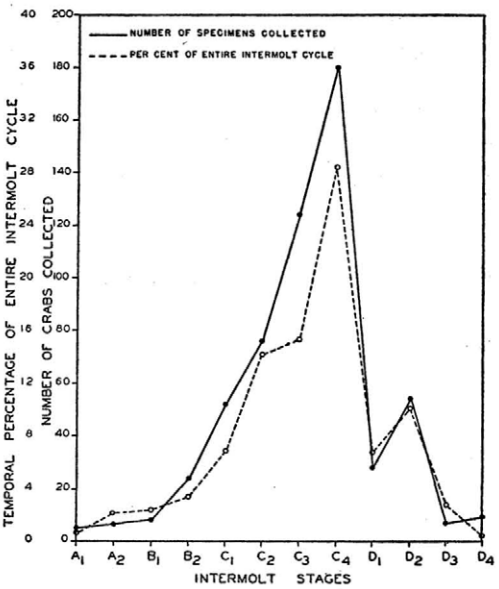


FIG. 2. A comparison between the frequency of occurrence of the intermolt stages in wild *P. crassipes* examined during August and the proportional extent of the individual stages with respect to the time required for the entire intermolt interval ascertained from captive crabs during the same seasonal period. The solid line represents the frequency of wild crabs in the various intermolt stages; the dashed line indicates the proportional amount of the intermolt interval assigned to the various stages.

in stage C_4, while stages D_1 and D_2 each contained one berried crab. It seems apparent, therefore, that ova are extruded onto the abdominal endopoditic setae during stage C_3 and are normally hatched prior to the attainment of stage D_1. In view of the facts that the incubation period of the ova has been found to range from 25 to 30 days (see p. 201), that the normal intermolt interval in female crabs ranging from 16 to 40 millimeters in carapace breadth varies from 23 to 40 days (Table 3), and that stages C_3 and C_4 combined comprise approximately one-half of the entire intermolt cycle, it is quite evident that ovigerous females undergo an abnormally prolonged intermolt interval.

Behavior patterns of *P. crassipes* are obviously dependent to a greater or less extent upon the intermolt stage at any given time. It was observed that certain crabs in the communities under observation tended to remain secluded in crevices throughout the daylight hours. During August, approximately half of the tide-pool population remained secluded, never entering into the active life within the pool or its environs. A reasonable explanation of this sequestering habit is found in Figure 7, wherein it is shown that more than 55 per cent of the total population of crabs was in a relatively soft condition (stages A_1–C_2). During diurnal hours crabs apparently seclude themselves immediately preceding ecdysis and remain concealed until stage B_1 is attained. Evidence for this inference was secured from the fact that diurnal collections of crabs in tide pools has failed to include crabs in stages D_4 to A_2. This concealment during daylight hours is almost certainly an act of self-preservation. A crab in stages D_4 to A_2 is virtually defenseless inasmuch as the chelae are supple and the muscular insertions are in a state of reduced efficiency because of the flexible integument.

Nocturnal collections, on the other hand, consisted of crabs in all stages of the intermolt cycle. The absence of light probably provides the animals with increased freedom of movement and safety because the vision of predators as well as of the crabs themselves, which are cannibalistic on occasions (see p. 179), is considerably reduced. Night, therefore, is the most opportune time to make collections of this species. A representative sampling of all intermolt stages may be made at this time, whereas it is virtually impossible to do so during daylight hours.

It is the writer's firm conviction that many types of experimental data may be accurately secured through the use of comparatively few animals if the intermolt cycle is correctly diagnosed. Therefore, by extending the knowledge of the intermolt cycle to the grapsoid group, a framework upon which to base both experimental and natural history data is provided. Observations in both the laboratory and field, particularly the former, will in most cases be inaccurate and misleading if the intermolt stage of the animals, which represents a clue to their physiological state, is not diagnosed and considered.

ECDYSIS AND ASSOCIATED PHENOMENA

One of the most significant features in the life history of the Arthropoda is the act of molting, an incident in, and an expression of, growth. Nowhere among the Arthropoda is the process so striking and abrupt as it is in the higher Crustacea. Notwithstanding the voluminous aggregation of literature concerning the life histories of crustaceans, few descriptions of the actual process of ecdysis exist, and none has been published upon the exuviation of grapsoid crabs. One of the objectives of the present study has been to describe meticulously ecdysis in *P. crassipes*. In addition, considerable statistical data pertinent to various aspects of the molt and its effect on the crab have been accumulated and set forth below. From the above-mentioned data, an attempt has been made to ascertain the age groups in the existing crab population, as well as the age–size relationship.

Réaumur (1712, 1719) was the first investigator to describe exuviation of a decapod crus-

tacean in detail, the exuviation of the river crayfish (*Astacus fluviatilis*). Later, Couch (1837) was amazed to find a perfect exuvia of the lobster (*Astacus europeus*) and was responsible for the initial inference that after a certain size is reached the lobster discontinues the molting act. His description of exuviation accomplished by the common edible crab, *Cancer pagurus,* in 1843 was the first account of ecdysis within the Brachyura. Salter (1860) read before the Linnaean Society an account of ecdysis in the lobster and described in considerable detail each precasting and casting activity, and emphasized that the observation was indeed rare. That he was entitled to this assumption is indicated by my experience with *P. crassipes* (see p. 160). Several later descriptions of the molting act of the lobster (Packard, 1886; Herrick, 1909; and Elmhirst, 1923), together with the description of ecdysis in *M. squinado* by Drach (1939), have served to provide a basis for comparison between the brachyuran and astacuran modes of exuviation.

Exuviation

Two distinct phases of ecdysis are apparent: (1) a passive phase (no significant muscular activity), initiated in *P. crassipes* approximately 1 day prior to the molting act and manifest by water absorption which serves to increase body volume and which exerts sufficient pressure to separate the epimeral line or pleural groove on the branchiostegites; (2) an active phase, which is identified by actual muscular activity significant to the molting act. The active phase is initiated immediately after the split along the pleural groove, and its termination is manifest by the complete exuviation.

Crabs used in the study of ecdysis were reared in individual aquaria tilted to provide deep sea water at one end and none at the other, thus closely simulating the natural water–air relationship of the normal environment. Many of the crabs resided in the aquaria in excess of 8 months, and in that interval successfully completed their fourth molt. The laboratory diet consisted of small pieces of fresh liver offered once daily, after which the water was changed. To facilitate observation of the molting act as well as other behavior traits, a shelf with a glass bottom was constructed directly above the author's desk, thus providing a means of constant observation for most of the day. It was found that observation from the ventral aspect provided a maximum opportunity to view the details of ecdysis.

Both behavioristic and morphological changes are manifest prior to the impending molt. For 4 or 5 days preceding the molting act crabs above 10 millimeters in width cling to a corner of the aquarium and ordinarily refuse food, but exceptions were encountered in which a small quantity would be eaten until 2 days prior to the molt. This abstinence from feeding is conspicuous because the animals are normally voracious, actually leaping to seize suspended food. Crabs below 10 millimeters in width regularly consume food until 2 days before ecdysis without exhibiting signs of inertness, a characteristic undoubtedly stemming from the shorter intermolt interval undergone by small individuals. The abstinence from food and the general seclusiveness seem to be natural phenomena common to both astacuran and brachyuran types. Elmhirst (1923) and Herrick (1909) described identical reactions in the lobster, while Broekhuysen (1941) indicates similar habits for *Cyclograpsus punctatus* M. Edw. on the South African coast. Muscular activity in *P. crassipes* virtually ceases; the crab will move but slightly if disturbed the day preceding the molt. The diminished activity preceding the molt was likewise noted by Hay (1905) for *Callinectes sapidus,* and undoubtedly results from the transitory condition of muscle insertions as they change from the old integument to the new. It is apparent that movements by crabs in this condition would be decidedly ineffectual.

A trio of morphological signs indicative of the impending molt are relatively precise in this species. The first, and most perceptible change, is that in the pigmentation, which, al-

though less pronounced than in some astacuran forms (the lobster, Herrick, 1896, and Elmhirst, 1923; and the crayfish, Braun, 1875), is distinctive. Like *C. punctatus, P. crassipes* becomes drab, losing the characteristic luster of the integument so apparent prior to stage D_3. In addition to the pigmentary deposition in the new integument during D_3 and D_4, the opacity is probably also the result of the dissolution of the deeper layers of the old integument. A second morphological indicator of the impending molt is the resorption of the lime salts in certain areas of the integument; namely, the branchiostegites, the sterna, and the basi-ischiopodite and meropodite of the chelae (Fig. 3, R.). The epimeral lines become desclerotized, allowing the upper and lower halves of the branchiostegite to be forced apart as a result of the increased pressure of the haemocoelic fluid. This desclerotization occurs several days prior to the molt and may be discovered by applying slight pressure on the pleural groove. Approximately 3 days before the molt, the pressure will result in a precocious schism along the groove. A third morphological sign of the premolt phase is the friability of the carapace. Among specimens collected in the field, many had carapaces which cracked as they were grasped. Upon examination they were found to be in stage D_3. This significant character was utilized by Olmstead and Baumberger (1928) as the criterion upon which the stage "pillans" was based. Crabs of economic importance are aptly designated "peelers" in this stage because the old integument may be picked off to reveal the lustrous new integument underneath.

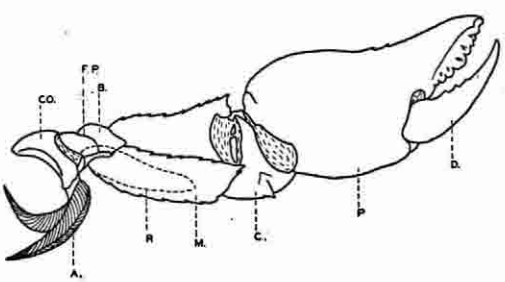


FIG. 3. The anterior aspect of the right cheliped of *P. crassipes*. A., arthrobranch; B., basi-ischium; C., carpus; CO., coxa; D., dactylus; F.P., fracture plane; M., merus; P., propodus; R., resorption line.

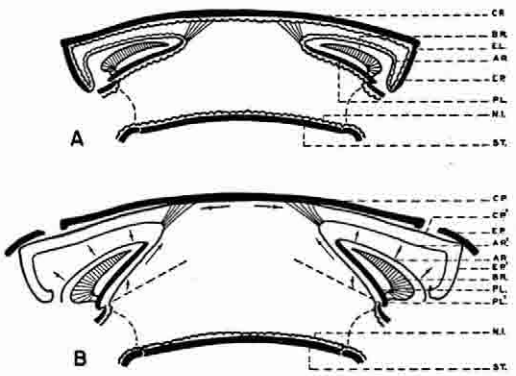


FIG. 4. A diagrammatic indication of the expansive movements occurring during the passive phase of ecdysis. Diagram A exhibits the relationship of the old and new integuments prior to ecdysis. Diagram B shows the relationships at the termination of the passive phase. AR., arch of branchial chamber; AR'., new arch of branchial chamber; BR., gill; CP., old carapace; CP'., new carapace; E.L., epimeral line; EP., epimeron; EP'., new epimeron; N.I., new integument; PL., pleural wall; PL'., new pleural wall; ST., sternal plastron.

On several crabs, the separation of the notal and pleural halves of the branchiostegites occurred a day prior to the active phase of the molting act. As the rift between the two halves of the branchiostegite widens, the gap between the two becomes continuous with the transverse lacuna between the posterior edge of the carapace and the first abdominal tergite. The elevated carapace resembles the lid of a box hinged at the anterior end of the animal, and underneath the old integument may be seen the new, somewhat wrinkled one. The expansive movements within the body of a crab undergoing ecdysis are diagrammatically indicated in Figure 4. The arrows indicate vertical and lateral expansion. The new, underlying integument is thin and wrinkled prior to the splitting of the epimeral line (Fig. 4 A), after which the old, thicker carapace is elevated allowing the new integument to stretch to the size to which it will eventually harden (Fig. 4 B).

Late in the passive phase the epimeral split extends anteriorly almost to the mouth. Some inconsistencies with respect to the origin of the

schism appear in the literature. Pearson (1908, on *Cancer pagurus*) and Hay (1905, on *Callinectes sapidus*) contend that the epimeral fracture appears first at the anterior end of the groove near the oral region and extends posteriad to connect each end of the gap between the posterior edge of the elevated carapace and the first abdominal tergite. Churchill (1918, on *C. sapidus*) refutes Hay and suggests that the converse is true. This study on *P. crassipes* definitely corroborates Churchill's findings. Many of the crabs which succumbed during the passive phase of the molt show the fracture in several stages of its splitting process; each fracture is oriented from the posterior to the anterior direction. Indeed, one may gently elevate the carapace and observe the actual splitting anteriorly.

Resorption of lime salts from the sternal integument is not apparent externally until the onset of the active phase of ecdysis. A split between the fused post-oral cephalothoracic and the fourth thoracic sterna, together with a schism along the mid-sternal line at the junction of the right and left sterna, is visible at the time the limbs are withdrawn. Slight pressure on these desclerotized areas prior to the molt likewise serves to detect the impending molting act.

When the elevated carapace reaches an angle of approximately 30° as a result of increased body expansion, the pereiopods are moved slightly, simulating walking movements, and a depression appears to one side of the cardiac area in the new integument. This initial depression disappears, but concurrently a new depression is developed on the opposite side of the cardiac area; each individual depression persists approximately 10 seconds and recurs rhythmically for a period of about 7 minutes in an average-sized female crab of 24.6 millimeters in width. A smaller crab with a carapace breadth of 7.2 millimeters was observed to complete its active phase of exuviation in 3 minutes and 10 seconds. Drach (1939) reports that the pulsations in *M. squinado* vary from 10 to 15 minutes. He further states that the alternating depressions are the result of muscle contraction in the coxopodites and basipodites of the thoracic appendages, and that these particular muscular movements are the principal ones occurring during the active phase. The muscles mentioned take origin on the endopleurites and endosternites, neither of which has appreciable rigidity at ecdysis; consequently, these newly formed skeletal elements offer less resistance to the contraction of the muscles than their insertions on the new integument of the coxopodites and basipodites which are still ensheathed by the old integument. Inasmuch as the endoskeleton and exoskeleton are continuous integumental structures, one would expect that particular part of the carapace (cardiac area) to be moved concurrently with the adjacent pleural wall. Since all of the muscles inserting on the coxa and basis of the various pereiopods take their origins in the same area of the pleural wall, and since the pleural wall is bound to the cardiac area of the carapace by a nonsclerotized portion of the integument, it is obvious that the depression occurring in the cardiac area during ecdysis will take place in that area only regardless of which legs are being withdrawn from the old integument. The hydrostatic pressure within the haemocoelic cavity forces the depression to disappear when the muscles on that particular side become quiescent.

The resultant accomplishment of these pulsations mentioned above is the withdrawal of the fourth and fifth pereiopods from the old integument. When the coxae and basipodites of the remaining legs are withdrawn, a rotation of the freed segments occurs in a manner suggestive of an attempt to release the distal podomeres from their sheaths. As the podomeres are successively withdrawn they quickly become distended with haemocoelic fluid and are thereby stiffened to assist in exerting a tug on those remaining in the old sheath.

The fifth pair of walking legs is the first pair to be withdrawn because withdrawal activity starts there, and also, perhaps, because they are the shortest pair. However, all undergo simultaneous exuvial progress which ultimately

results in complete consecutive withdrawal of all pereiopods from the fifth pair to the chelae. Special difficulties in withdrawal are presented by the chelae because of the enlarged distal podomeres. Special lines of absorption on the coxa, basi-ischium, and merus have been mentioned previously (Fig. 3, R.). This resorbed line fractures to release a roughly triangular flap of integument. This flap is hinged at the junction between the merus and basi-ischium and the anterior portion of the line of absorption on the merus. The lines of absorption on the basi-ischium and coxa fail to fracture but become very soft and pliable.

The frequency with which the animals undergoing ecdysis lose one or more limbs illustrates the critical nature of exuviation in the general welfare of the individual. A cursory examination of several exuviae which contained chelae of crabs unable to withdraw them from the old exoskeleton revealed that the lines of absorption were hard, with resorption insufficiently advanced to effect the fracture, which indicated that resorption of calcium salts in the old integument was apparently impeded in some manner. The severence of appendages through the inability to withdraw them successfully has been recognized previously and designated "exuvial mutilation"; however, a more precise expression, "exuvial autotomy," suggested by Drach (1939) seems more appropriate.

After the successful withdrawal of the posterior four pairs of appendages, the old sternal integument is separated from the new. An elongation of the body, together with an upward and backward movement of the crab, combines to exert the necessary pull on the abdomen, which is subsequently withdrawn. The limbs are then directed forward. An ejection of amber fluid from the mouth occurs, after which a few seconds of quiescence ensues. After this brief period of inactivity, rapid movements of the limbs occur in a forward–backward motion. This activity is repeated two or three times, and serves to remove the buccal appendages and the chelae. The amber ejection is probably the material in the stomach which must be expelled with the old epithelium. The chelae are decidedly wrinkled as they are exsheathed because of the forced expulsion of the haemocoelic fluid to enable the bulbous distal end to be withdrawn through the small coxal opening. However, they become turgid immediately after ecdysis.

An examination of the exuvia shows that the apodemes and branchial filaments are preserved in approximately their original morphological position. Since it is not possible to observe the exsheathing of the apodemes and gills this phenomenon must be interpreted through critical study of the morphological characteristics of the exoskeleton.

The apodemes are invaginations of the integument, each lamina being formed by two thicknesses of sclerotized integument united by their morphologically external surfaces. Prior to the impending molt new strata are secreted and these strata (the epicuticle and pigmented layer) of the new integument lie internal to the old integumental strata of the apodemes (Fig. 5); during the withdrawal of the appendages the new apodeme is slipped off the old, which is rigidly attached to the exuvia. Mechan-

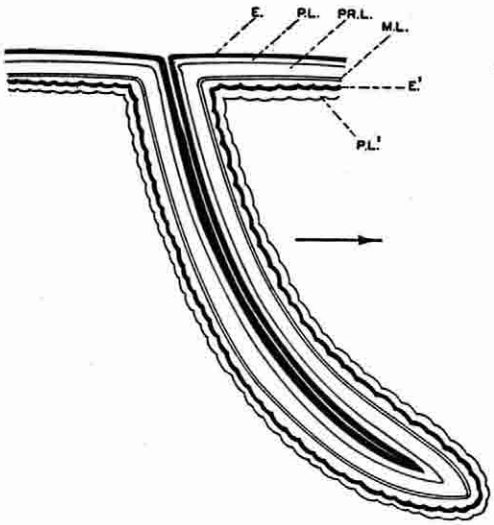


FIG. 5. A diagrammatic section through an apodeme to show the integumental strata. The arrow indicates the direction of withdrawal at ecdysis. E., epicuticle; E.', new epicuticle; M.L., membranous layer; P.L., pigmented layer; P.L.', new pigmented layer; PR.L., principal layer.

ically, the casting off of the old apodemes is facilitated because they are generally directed toward the basal portion of the appendage; therefore, the withdrawal of the new appendages presents no special difficulty. A comparison between the apodemes of a skeleton and those of an exuvia shows that those apodemes not directed posteriorly are either resorbed in stages D_3 and D_4 or are secondarily oriented in a posterior direction after the sternal schism.

The apodemes which partition the two sides of the thorax offer more difficulty to successful exuviation than those of the pereiopods. They consist of invaginations of the endosternites and pleural walls and serve as the attachment for the origins of the muscles of the basipodites and coxopodites. It was stated above that when the body is elevated above the old sternal floor, this elevation, in conjunction with anteroposterior elongation, serves to disengage the apodemes which are directed posteriorly after the sternal schism. A comparison of the endoskeletal structure of a normal animal with that of an exuvia shows that the normal structure has been altered during ecdysis. This alteration is manifested in partial or total resorption in certain endoskeletal areas. Without this resorption, molting would not be possible because the transverse apodemes together with their ramifications would hinder the withdrawal of tissues without injury. The occurrence of the sternal schism in *P. crassipes* serves to reduce effectively the degree of resorption which would otherwise be requisite providing the sternum remained entire.

The structural association of the phyllobranchiate gills with the proximal portion of the gill-bearing thoracic appendages makes it imperative that the withdrawal of the gills coincide with the onset of the active phase of ecdysis. Inasmuch as the brachyuran gill is composed of two series of lamellae inserted on a median raphe, the lamellae must flatten and be drawn through the median raphe over the orifice of insertion on the skeleton. The branchial apertures of the skeleton are small, but the edges are rounded so that the gills pass through them without great difficulty. Subsequent to the complete withdrawal of the new gill from its old integument, it remains wedged between the old and new epimeral walls until the body is elevated to a position above the old exuvia and until the proximal podomeres are moved to the upper level of the old pleural wall. It is evident that the abnormal torsion undergone by the gills during ecdysis might conceivably provide respiratory difficulties which would designate ecdysis as a critical interval in the life of the animals. Supportive evidence for the above statement was secured upon the compilation of mortality data for crabs confined to the laboratory. Of a total of 78 fatalities among laboratory animals, 61 (78.2 per cent) occurred prior to complete withdrawal of the pereiopods. Therefore, these deaths took place when the gill lamellae were in an abnormal, contorted condition.

One of the features of ecdysis which invites discussion is the origin of the mucilaginous material which covers the inner surface of the exuvia and the external surface of the new exoskeleton. Its apparent function of lubrication of the frictional surfaces during ecdysis is manifestly significant. Its initial appearance in *P. crassipes* occurs when the rift between the posterior edge of the carapace and the first abdominal tergite shows a tenuous membrane stretched across it. With further separation between the carapace and the first abdominal tergite the membrane fractures. There is little doubt that this mucilaginous layer is probably the same as that first described by Réaumur (1712), who recognized its apparent function. Vitzou (1882) suggested that the mucilage was secreted by the epithelium, in which case it would have had to penetrate the two new integumental strata prior to reaching its definitive location between the old and new integuments. Herrick (1896) subsequently proved Vitzou's contention erroneous because this layer bore the impress of a mosaic of cells, and, in view of its cellular composition, postulated that it was either the first secreted portion of the new integument or the internal membranous

stratum of the old. Yonge (1932) provided proof to substantiate the second possibility set forth by Herrick. Furthermore, he asserted that the internal membranous layer was dissolved by the action of cells which passed into it from the epithelium prior to and during ecdysis. Drach (1939) agreed with Yonge concerning the stratum involved but found no basis for the mode of gelatinization suggested by that investigator. After a meticulous histological study of the internal membranous layer during stages D_1 to D_4, Drach found that the lymphocytes were irregularly grouped and insufficient in numbers to effect a uniform transformation of this stratum into a jellified condition. He maintained, moreover, that the homogeneity of this jellification presupposed the intervention of some chemical agent secreted by the epithelial cells. In the Insecta an enzyme, chitinase, causes an analogous resorbing action. Wigglesworth (1933) stated that chitinase is a glandular secretion of the epidermis; therefore, it is not unreasonable to assume that in the Crustacea a comparable enzyme is secreted by epithelial cells or glands which induces the gelatinization so significant to the success of exuviation.

The relatively high exuvial frequency coupled with the extreme infrequency of observations of the molting act seem to present at least two implications. First, ecdysis must occur very rapidly, or second, ecdysis must take place during times when the animals are not under observation. It is the writer's opinion that the initial hypothesis may be discounted (see p. 155). The latter supposition, however, is adequately supported by data compiled from animals confined to laboratory aquaria. Of the 141 molts which occurred among captive crabs, all but three took place between 8:00 P.M. and 5:00 A.M.; thus, 97.9 per cent of the molts occurred during nocturnal hours. Broekhuysen (1941) and MacKay (1942) also noted that most of their captive specimens underwent exuviation at night. Early suggestions which coupled molting with moon and tidal effects are contradictory, devoid of evidence, and untenable in the present investigation; therefore, these conjectural causes are discarded forthwith in favor of the evidence presented below. It has been pointed out previously that crabs in stages A_1 and A_2 are extremely susceptible to injury and possible fatality if attacked by predaceous species during the first 6 to 10 post-exuvial hours. The reduced vision of littoral predators, including cannibalistic *P. crassipes* and the ubiquitous Norway rat (*Rattus norvegicus*), is certainly advantageous to the comparatively defenseless, recently molted crabs. The several nocturnal hours following the molt undoubtedly provide substantial, but quantitatively unknown, protection for this species. Moreover, the elevated littoral position preferred by *P. crassipes* markedly exposes them to the predation of numerous gulls. Therefore, if molting were undergone during the day to any appreciable extent, the mandatory position in the tide pools, at least for a portion of the early, post-exuvial hours, would place these crabs in certain danger which would be magnified because of the subnormal locomotory powers of the soft crabs.

Although considerable variability occurs in the time required for maximum post-exuvial expansion, an indication of typical expansion with respect to the time intervals involved may be secured from Figure 6, which illustrates these data derived from three distinct sizes of crabs selected to emphasize the comparative aspect. Pre-exuvial carapace breadths were: crab A, 6.3 millimeters; crab B, 25.0 millimeters; and crab C, 35.8 millimeters. The first post-exuvial measurement of crab A was made immediately after the molt and revealed a 4.7 per cent size increment with respect to initial width at that time. Crabs B and C were not measured until 2 hours after the completion of ecdysis. Regardless of the initial carapace width, the greater part of post-exuvial expansion occurs prior to the third hour after ecdysis. Actually, considerable expansion occurs before exuviation is completed, because swelling of the body accompanies the active phase of exuviation. However, the expansion is not measurable until ecdysis terminates.

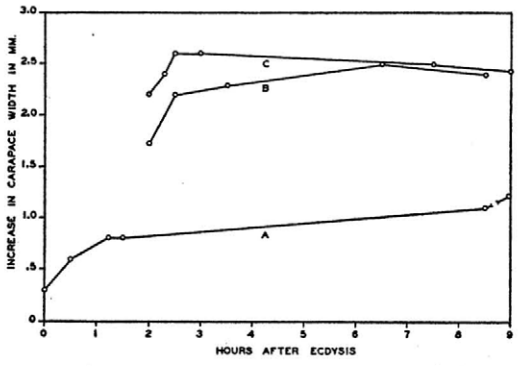


FIG. 6. Typical post-exuvial expansion for three distinct sizes of crabs. See text for details.

The impregnation of carbonates in the exoskeleton of *P. crassipes* begins at the tip of the chelae and becomes apparent about 36 hours after ecdysis. However, the insufficient sclerotization proximal to the tips prevents the average-sized crabs (32.0 millimeters) from employing these structures defensively until the third or fourth day after the molt. The pinch is ineffective on the fourth day but becomes progressively more effective until normalcy is nearly achieved on the twelfth day. Inasmuch as the carpus and merus of the ambulatory legs are the final portions of the integument to become sclerotized (Table 2), the ability of *P. crassipes* to employ these pereiopods effectively before the broadened sides have attained rigidity is attributable to their shape and direction of movement. The edges of these flattened podomeres are oriented approximately perpendicular to the substrate, and the long axis of the appendages assumes a lateral position which forms a right angle with the main axis of the animal. This orientation is significant because the direction of locomotion is likewise lateral (see p. 177). The legs are incapable of bending on their edges, but flex readily on their lateral surfaces prior to total sclerotization. Locomotion in the early post-molt interval is possible and effective because of the shape and orientation of the ambulatory appendages.

Seasonal Exuvial Periodicity

The recorded data indicate that ecdysis in Crustacea inhabiting temperate areas occurs more frequently during the warmer period of the year. Herrick (1909), Churchill (1918), and Broekhuysen (1936, 1941) concur in this belief; the former two authors further stated that most of the molts occur on the Atlantic coast of America from June to October, while the latter worker graphically illustrated a more extended molting season for the South African *C. punctatus*. The molting incidence of *P. crassipes* simulates the more extensive seasonal type illustrated by *C. punctatus*.

The seasonal exuvial periodicity of *P. crassipes* under normal environmental conditions was ascertained through collections of crabs which were subsequently examined for their intermolt stage. Although sex was disregarded in the above analysis, it must be pointed out here that slight abnormalities in the molting incidence are exhibited by ovigerous females (see p. 154). These deviations from the normal cycle of successive molts are, however, insufficient to alter the general chain of events. Ecdysis occurs most frequently during August, September, and October; but considerable exuviation is apparent in all except the winter months, November through February. The exuvial periodicity presented here is particularly apparent to the frequent intertidal-pool visitor. The early morning receding tide discloses a far greater number of exuviae in the pools during the warmer months of the year than during the cooler winter season. The rather lengthy span of relatively high molting frequency is probably associated with the small range of temperature characteristic of the geographical range of this species.

The comparatively significant rôle of temperature fluctuations in the physiology of poikilothermal species, together with the fact that temperature is one of the most widely fluctuating physical characteristics in the environment of these littoral animals, provides the basis for a comparison between thermal fluctuation and seasonal molting periodicity. The temperature of the surface water was selected as that most appropriate for this purpose. The figures presented were secured from the U. S. Coast and

Geodetic Survey report for the year 1939. The readings are surface temperatures taken at Fort Point, San Francisco Bay. The figures correspond closely to those published by Sumner *et al.* (1914), and to those taken just outside the Golden Gate by the U. S. Weather Bureau during the years 1915 to 1924. A marked coincidence is noted between the exuvial periodicity and the mean surface temperatures for the annual period (Fig. 7). It is significant that the apices of thermal and exuvial activity fall exactly in line. Ecdysis seems to be perceptibly slowed when the surface temperature drops below 14° C., indicating that the physiological processes, presumably those participating in endysis, are slackened in pace. Supportive evidence for this thesis was secured from several captive crabs of similar size upon which a careful record was kept concerning their intermolt development through the cooler months. The normal intermolt interval for crabs of 24 to 30 millimeters in width varies from 45 to 60 days during the relatively warm midsummer months. However, the captives which molted in November and early December had only reached either stage C_4 or D_1 more than 3 months later. The intermolt records of these captive crabs show that endysis is slackened to approximately one-half the pace typically exhibited during warmer seasons.

To check the findings described above, the exuvial frequency of captive crabs together with the temperature fluctuations of the laboratory water were recorded monthly. These data are combined with the field data shown in Figure 7.

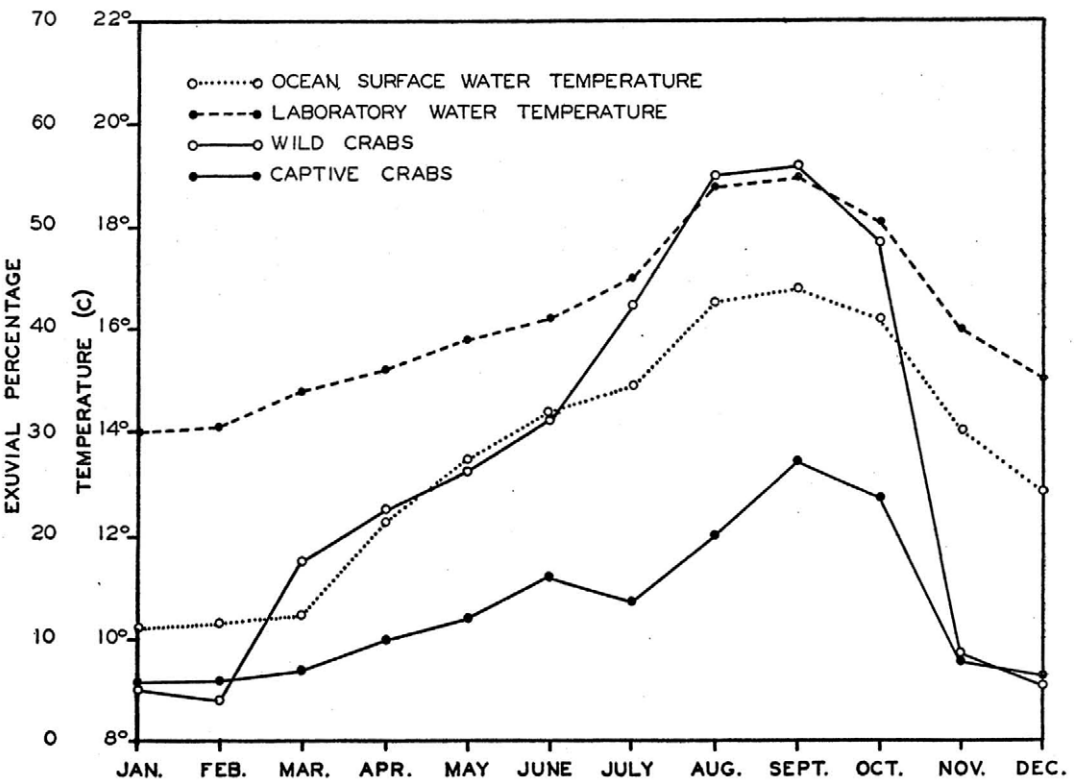


FIG. 7. A comparison between ocean surface and laboratory water temperature and the annual exuvial incidence in wild and captive *P. crassipes*, respectively. The surface temperature readings represent the monthly mean temperatures recorded at Fort Point, San Francisco Bay, 1940.

Variation in Post-exuvial Size Increment

Considerable variation in the size increment after ecdysis seems apparent both between different species of crabs and between different size groups within a species. In addition, a slight differential variation in size increments is apparent between the sexes. Williamson (1903) and Pearson (1908) investigated the post-exuvial size increment in *C. pagurus* and presented statements which implied that the size increment at each successive molting period was constant. When the data presented by the above authors were plotted by Olmstead and Baumberger (1923) it was shown that their conclusions were erroneous. Further, the latter workers demonstrated that the smaller and presumably younger specimens increased to a relatively greater extent than did the older and larger specimens. Broekhuysen (1941) and MacKay (1942) found a similar condition in *C. punctatus* and *C. magister,* respectively, while Gray and Newcombe (1938) showed the converse to be true for *C. sapidus,* but to a lesser extent in males than in females.

Individual variability, both with respect to animals of similar size and animals of different sizes, has been conspicuous throughout the present investigation of the molting characteristics of *P. crassipes.* An examination of Figure 8 will show that variability in post-exuvial size increment for both wild and captive crabs above 10 millimeters in carapace breadth may reach as high as 200 per cent. Smaller captive animals exhibit a variation in excess of 400 per cent. It is also apparent that there is a proportionate decrease in the percentage of post-exuvial width increments with age. However, when actual width increments instead of ratios were plotted, it was seen that young crabs (below 15 millimeters in breadth of the carapace) increase in size at ecdysis up to a maximum of 2 millimeters; middle-sized crabs (between 15 and 35 millimeters in breadth of the carapace) show increases up to 4 millimeters following the molt; while very large crabs (above 35 millimeters in breadth of the carapace) show much less growth at the molt and seldom increase in size more than 2 millimeters in breadth of the carapace.

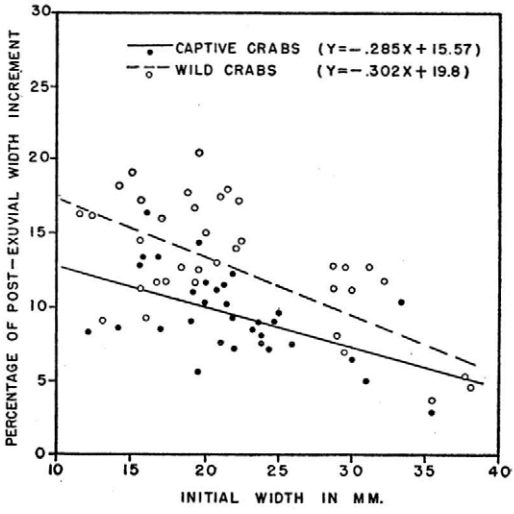


FIG. 8. Scatter diagram comparing the variation in percentage of the post-exuvial width increment in wild and captive crabs above 10 mm. in breadth of the carapace. The regression lines were fitted by the method of least squares.

Of great significance is the demonstrated fact (Fig. 8) that the laboratory environment, in spite of the fact that it was meticulously regulated, is dissimilar to the natural environment: this is shown by the generally smaller growth increment (size for size) for captive crabs as compared with wild crabs. The mean growth increments for all captive crabs and for all wild crabs above a carapace breadth of 10 millimeters were computed and the standard "t" test was applied to the two sets of data. The difference between the means of the two sets of data was found to be highly significant statistically ("t" $=7.27$: "t" for $0.01 = 2.8$). The regression lines shown in Figure 8 illustrate this point graphically. The great similarity in structure and response of the various species of the higher Crustacea suggests a strong possibility that the debilitating effects of laboratory life will affect them all. It is of great importance, then, that experimentalists treat results obtained in the laboratory with reserve and caution before the precise effects of confinement are well known.

A great number of the captive crabs maintained in the laboratory were injured specimens (individuals which had lost one or more pereiopods). The post-exuvial size increment data for these individuals were recorded separately and compared with the data derived from normal captive animals. It was found that, in general, the magnitude of variation in size increments of injured crabs is less than that for normal captives; in addition, the individual post-exuvial size increments are significantly less. Underlying factors responsible for this phenomenon seem at this time to be largely conjectural. MacGinitie (1937) infers that mutilation may stimulate molting in *Crangon californiensis* as well as in other macrurous forms. There are, however, no data presented to support this inference. Several controlled experiments on regeneration in *P. crassipes* indicate that both acceleration and slackening of the intermolt cycle may occur, depending upon the degree of integumental development at the time of mutilation (see p. 194). Mutilation prior to stage C_3 lengthens the intermolt interval in *P. crassipes*. Limbs severed during the early C_4 stage show an accelerated regeneration, but the intermolt interval is normal. It would seem that an accelerated intermolt cycle would be advantageous after the loss of one or more appendages because it is certain that maximal efficiency in activities concerned with general welfare would be dependent upon the entire complement of appendages. However, further study is required for a satisfactory solution to this phase of the problem.

Comparative studies on the post-exuvial width increments of male and female crabs indicate that no significant variation between the sexes occurs until an initial width of approximately 25 millimeters is attained. The foregoing information was secured by plotting initial and post-exuvial widths of both sexes from recent molts and exuviae collected in the normal habitat (Fig. 9). The ratio of initial to final width remains approximately identical for both sexes until two rather distinct ratios become apparent, with the digression taking origin in those crabs about 25 millimeters in initial width. The smaller post-exuvial size increments of females after attainment of sexual maturity show why representatives of this sex are invariably smaller than males in a given intermolt cycle after the tenth to twelfth molt (Table 3), and, in addition, show why the largest specimens collected are always males (Fig. 9).

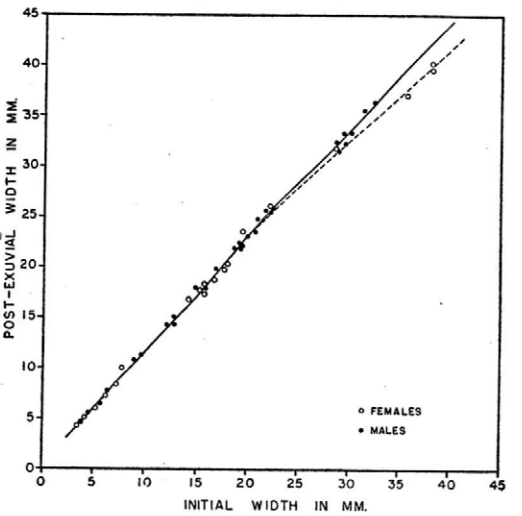


FIG. 9. Sexual dimorphism in post-exuvial width increments for *P. crassipes*. These data are derived from measurements of recently molted wild crabs for which the exuviae were found. The lines have been fitted by eye.

Exuvial Frequency

Prior to a consideration of the number of exuvial stages during the life span of *P. crassipes*, it is necessary to point out that reproductive activity, to a certain extent, alters the usual exuvial succession in females. There is evidence to indicate that coition occurs by the time the female reaches stage A_2 (see p. 199). It has been shown previously in this paper that the ova are extruded onto the pleopods during stage C_3, and are subsequently hatched during stage C_4. Approximately 25 days are required for an average-sized adult female to reach stage C_3 at which time ova would be extruded onto the pleopods. About 30 days are required for the incubation period, which is concluded toward the end of stage C_4. Some 10 to 15 days

are then required for the changes undergone during period D. A minimum total intermolt interval of 65 to 70 days is therefore required for the breeding females. Non-ovigerous captives of similar size require an interval of but 40 to 50 days. This delayed intermolt interval of ovigerous females, coupled with the fact that exuvial incidence as well as spawning frequency is highest at this season, indicates that the usual temporal sequence of ecdysis is interrupted to such an extent that the total number of expected molts is decreased by one each year subsequent to maturity.

On the basis of the data set forth in Figure 9 it is possible to calculate the number of intermolt intervals which will occur in crabs from 3.4 millimeters or more in initial width to the maximal adult size. For example, let us assume the initial width of a given crab to be 5.5 millimeters. By placing a line along the ordinate of the 5.5-millimeter point, it will be found that the growth curve will be intersected at a point which corresponds to 6.6 millimeters on the abscissa. Then, assuming the latter width to be the next initial width, the corresponding post-exuvial width (8.0 millimeters) may be similarly located. The growth curve, therefore, enables one to calculate the entire sequence of molts from the first crab stage to the termination of growth. The calculated size increments based on the curves shown in Figure 9 check accurately with the size increments of wild crabs which underwent ecdysis in the field. The post-exuvial size increments of recently molted wild crabs in representative size categories provide the following data which closely adhere to the expected size increments as calculated from the growth curve: small crabs of undetermined sex increased in size from 4.8 to 5.8 millimeters; male crabs increased from 19.7 to 22.6 millimeters, and from 33.6 to 37.4 millimeters; and female crabs increased from 7.7 to 9.0, 21.0 to 24.0, and 30.0 to 32.4 millimeters.

Calculations made in the manner outlined above demonstrate that females with an initial width of 3.4 millimeters undergo 21 additional molts before attaining maximal size, as contrasted to 18 for males of corresponding initial width. These data are presented together with other pertinent data in Table 3. The growth curve for females, presented in Figure 10, takes into account the fact that female crabs apparently undergo a greater total of molts than do males. The curves, of course, represent an estimation of the number of molts. Furthermore, it is apparent from the discussion above that considerable individual variation may and does present itself; nevertheless, on a basis of the recorded observations, the curves indicate the type of growth that characterizes this species.

Age

The interval between hatching and the attainment of the adult or true crab stage must be known in order to present accurately an age–size scale. It was impossible to determine this span for *P. crassipes* because of laboratory deficiencies. However, Hart (1935) investigated the larval development of *Hemigrapsus nudus* and *H. oregonensis,* and the intervals given for these two near relatives probably approximate the corresponding developmental interval for *P. crassipes.* Hart described one prezoeal stage, five zoeal stages, and one megalopal stage for both species of *Hemigrapsus.* Moreover, it was shown that the larval stages of the congeners were virtually identical both in structure and in time of development. Therefore, if the larval development of *P. crassipes* is similar to that of its two near relatives, seven molts would occur in the interval between the emergence from the egg and the attainment of the first crab stage. These data, coupled with those presented in Table 3, indicate that for a male to attain the apparent maximal size of 47.0 millimeters (the largest size recorded for males) it must successfully undergo about 25 molts; a female, to attain the maximal size of 44.0 millimeters (the largest size recorded for females), must undergo about 28 molts.

TABLE 3

SUMMARY OF THE ESTIMATED NUMBER OF MOLTS, THE ESTIMATED NUMBER OF DAYS IN THE INTERMOLT INTERVAL BETWEEN EACH SUCCESSIVE EXUVIATION, AND THE SIZE INCREMENTS AT EACH EXUVIATION FOR BOTH SEXES OF *P. crassipes* FROM HATCHING TO THE ATTAINMENT OF MAXIMUM SIZE.

INTERMOLT INTERVAL	MOLT NUMBER	FEMALES		MALES	
		Number of Days	Size Increment*	Number of Days	Size Increment*
Larval stages†		35		35	
1st to 2nd	1	18	3.4– 4.4	18	3.4– 4.4
2nd to 3rd	2	19	4.4– 5.5	19	4.4– 5.5
3rd to 4th	3	21	5.5– 6.8	21	5.5– 6.8
4th to 5th	4	22	6.8– 8.2	22	6.8– 8.2
5th to 6th	5	23	8.2– 9.7	23	8.2– 9.7
6th to 7th	6	24	9.7–11.4	24	9.7–11.4
7th to 8th	7	25	11.4–13.2	25	11.4–13.2
8th to 9th	8	26	13.2–15.1	27	13.2–15.1
9th to 10th	9	27	15.1–17.2	29	15.1–17.2
10th to 11th	10	27	17.2–19.3	31	17.2–19.3
11th to 12th	11	28	19.3–22.0	33	19.3–22.0
12th to 13th	12	29	22.0–25.0	35	22.0–25.2
13th to 14th	13	30	25.0–27.8	37	25.2–28.2
14th to 15th	14	31	27.8–30.3	40	28.2–31.3
15th to 16th	15	32	30.3–32.7	44	31.3–34.7
16th to 17th	16	33	32.7–34.8	45	34.7–38.5
17th to 18th	17	36	34.8–36.7	47	38.5–42.5
18th to 19th	18	39	36.7–38.4	50	42.5–46.0
19th to 20th	19	40	38.4–40.0		
20th to 21st	20	41	40.0–41.5		
21st to 22nd	21	45	41.5–42.8		
Total		652		652	

* The size increments are based upon the data set forth in Figure 9. All measurements represent the greatest carapace width in millimeters.

† The intervals shown for larval stages are based on those found by Hart (1935).

Hart (1935) found that the time interval from hatching to the first crab stage in *H. nudus* and *H. oregonensis* spanned 4 to 5 weeks. Each successive zoeal stage required more time than the one which preceded it. The present data, set forth in Table 11, indicate that the intermolt interval between the first crab stage and the second crab stage varies between 14 and 20 days, with a progressive increase in the intermolt interval with age. Captive crabs larger than 7 millimeters in width were reared under conditions slightly unfavorable to optimum growth; hence the intermolt interval of captive specimens spans a somewhat longer period than that characteristic of wild crabs. The chief value of the figures obtained from captive animals resides in the fact that they are maximal; consequently, they aid materially in computing intermolt intervals. Significant assistance was derived from the information on intermolt intervals of *P. crassipes* secured from wild specimens by Olmstead and Baumberger (1923). When the intermolt span for captive crabs was compared with that furnished by the above investigators for crabs of identical widths, it was found that the time involved for captive specimens was increased approximately one-third. A scale of intermolt intervals has been synthesized for both males and females and is presented in Table 3.

The usual method of plotting size–frequency data, to ascertain the age groups of which a population is composed, was employed on a collection of several hundred crabs taken during a 1-week period in August, and was found to yield confusing results. Histograms were drawn for each distribution, and the modal groups comprising the distributions were superimposed with a number of normal curves having different standard deviations and different areas,

in an attempt to identify and separate the homologous groups in this series of size frequencies. The method employed was that developed by O. E. Sette and used by Brock (1943) in his studies on the Oregon albacore fishery. Although the plotted data had trimodal characteristics, the differences in height between the modal and adjacent intermodal classes were slight and variable. It was impossible to fit any set of normal curves to the data.

Factors responsible for the absence of clearly defined age groups are undoubtedly associated with (1) the frequent exuvial periodicity for all age classes; (2) the variability in post-exuvial size increments; (3) the extensive breeding season.

Inasmuch as the number of molts and their corresponding intermolt intervals are approximately known, it was possible to designate graphically the size–age relationship. Since there is a period from November to March during which ecdysis is unlikely to occur, and since breeding females apparently lose one molt each year because of the extended ovigerous period, these modifications were incorporated into the size–age scale presented in Figure 10. The frequency with which ovigerous females were collected during each month of the year shows that June represents the mid-point in the breeding season; consequently, the curves for size and age stem from that period.

Several factors pertinent to growth and age are exhibited in Figure 10. First, three distinct age groups are represented, with crabs of both sexes attaining the supposed C_4T stage during the third year. Measurements of several thousand individuals collected during August, 1940, showed that the frequency of large male crabs fell abruptly at 40 millimeters width with the largest specimen taken measuring 47.0 millimeters, while the frequency of large female crabs descended rapidly from the 30-millimeter size with the largest specimen measuring 44 millimeters. Second, the crabs of both sexes about 13 millimeters in width may be considered to represent maximal size for first-year individuals; crabs between this size and 30 millimeters represent second-year individuals;

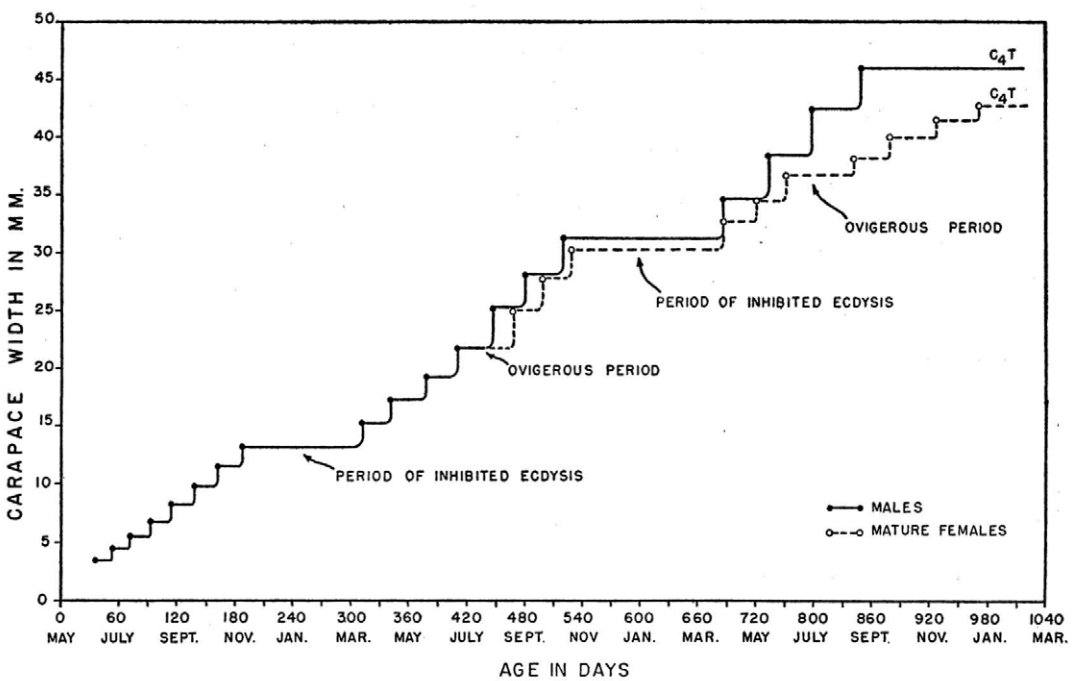


FIG. 10. Size and age curves for *P. crassipes*.

and crabs above this width seem to be third- or perhaps fourth-year specimens and show no evidence of impending ecdysis. Third, the curves indicate that size–age dimorphism first becomes apparent in crabs with a carapace width between 20 and 25 millimeters. Further, the data set forth in Figure 11 present evidence to show that this dimorphism occurs just subsequent to the onset of sexual maturity in females. These data were secured from 80 ovigerous females collected from August 3 to 10, 1940. In addition to establishing corroborative evidence with respect to size dimorphism, the data presented in Figure 11 show that the size span for ovigerous females is too extensive to fall within any single age group, but does coincide well with the data presented in Figure 10. Fourth, it is apparent that the size divergence between sexes, after sexual maturity in females, is associated with a successive proportional decrease in post-exuvial size increment. Notwithstanding all the variables attendant upon the growth of crabs, the life span and growth characteristics set forth above are, in general, characteristic of this species.

Comparative information on age investigations of other species of Brachyura is particularly significant because virtually all workers have followed different avenues of approach, yet nearly all obtained comparable results. Aside from the comparatively lengthy life span of 8 to 10 years for *Cancer magister* (MacKay, 1942), those known are very similar to that of *P. crassipes.* Hay (1905) and Churchill (1918) found a 3-year life span for *Callinectes sapidus* with mating and spawning initiated in the second year, and Broekhuysen (1936, 1942) discovered a similar span for *Carcinides maenas* and *Cyclograpsus punctatus.*

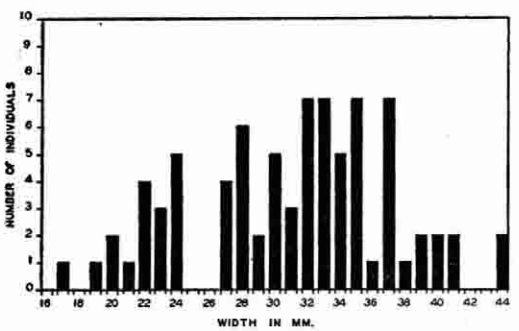


FIG. 11. Size frequency of ovigerous *P. crassipes* collected during August, 1940.

GENERAL HABITS AND BEHAVIOR

Visual, Chemical, and Tactile Senses

Observations and simple experiments performed with both captive and wild crabs indicate that the visual and tactile senses of *P. crassipes* are well developed, while the chemical sense seems to operate on a somewhat lower functional grade. The complex integration and mutual cooperation of all three senses are of such nature that an estimation of the degree of participation in an observed reaction can only be arbitrary at best.

Although visual acuteness among the Crustacea is doubted by many investigators, an observer of *P. crassipes* could scarcely fail to note their alertness. The stalked eyes are capable of considerable movement. At rest the normal, undisturbed animal will frequently move the eyes forward, backward, and laterally. These movements suggest a critical surveillance of the environment in an attempt to achieve the most acute images possible. When frightened, the animals lower the eyestalks laterally into a groove for their reception between the orbital and suborbital areas of the carapace. The faceted surface of the lowered eye receives protection from the orbital spine.

It is generally believed that the sharpness of any image recorded by this type of eye will depend upon the number of facets which perceive the object. Inasmuch as the number of facets engaged by an object varies inversely as the square of the distance, *P. crassipes* must be somewhat myopic. If the number of facets engaged by the object provides the lone criterion for visual acuteness, the rapid reaction of *P. crassipes* to persons walking at a distance of several yards is somewhat enigmatic. It would seem, therefore, that a moving object

stimulating a number of facets in rapid succession imparts an impulse to the central nervous system which results in a more extensive reaction than that resulting from the perception of stationary objects. Slight movements within a few feet of the animals elicit instantaneous responses; whereas considerable movement at a distance is required to obtain a response of similar magnitude. The greatest degree of visual activity in the faceted eye is achieved not only at short distances but, in addition, on that area of the eye which has the least curvature, since it is obvious that the greatest number of light rays emanating from an object will strike comparatively more ommatidia if the faceted surface is flattened. My observations coincided with the predicted response founded on the foregoing principles. Figure 12 is presented to demonstrate the curvature and extent of the faceted surface of the eyes of *P. crassipes* in several planes of vision. It is seen that the least faceted surface occurs on the medial portion of the eye (D); this is to be expected because the opposite eye receives visual stimuli from the identical angle. The dorsal surface (A) is strongly convex and slightly faceted. These data indicate that vision dorsad would be poor, a fact substantiated on numerous occasions while observing crabs from a vantage point directly above. Space does not permit a detailed presentation of these observations. The posterior region of the eye (E) is likewise strongly convex and provided with relatively few facets. Vision in a posterior direction does not appear to be acute, but it is difficult to effect successful observations because the posterior end of the crab is usually directed toward a sheltering area in the habitat. It would seem that the compensatory movements of the eyes (rotation of the eyestalk to direct highly faceted areas of the eye to new positions), which will be discussed below, serve to span the posterior direction effectively.

The anterior portion (C) of the faceted surface is much greater in comparative area and exhibits less convexity than the regions discussed above. Vision in the forward direction, therefore, would be expected to be good. This supposition has proved valid many times. The slightest movement of a person at a distance up to 30 yards elicits immediate response. Compensatory movements probably increase visual acuity in the forward direction because the animals seem somewhat more responsive to visual stimuli than one would expect from the number of facets located in the anterior portion of the eye. The outer or lateral (B) surface of the eyestalk is comparatively flat and completely covered by ommatidia. Observations indicate that visual acuity is most pronounced in the lateral direction, a predicted result based upon an examination of the morphological features of the eye. Further, it appears highly significant that the most effective visual surface lies in the plane of normal locomotion.

The compensatory movements of the eyestalks, such as those described for other Crustacea (Bethe, 1897; Cowles, 1908), occur in *P. crassipes* when they are tilted either from left to right or in an anteroposterior direction.

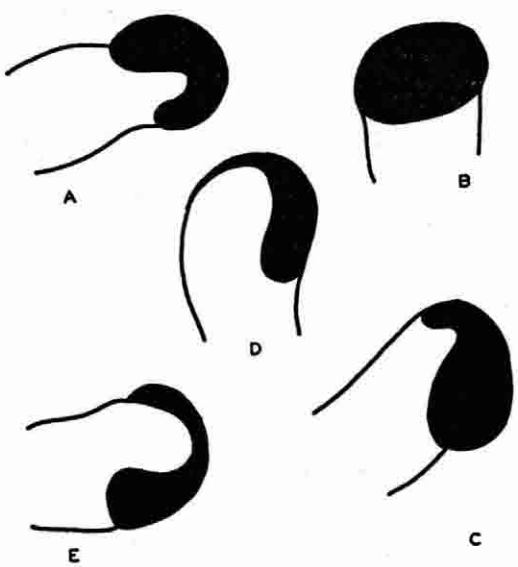


FIG. 12. Comparative amount of curvature and faceted surface on various aspects of the eye of *P. crassipes*. A, dorsal surface; B, outer or lateral surface; C, anterior surface; D, medial surface; E, posterior surface.

When the anterior end of the crab is tilted downward from the horizontal plane, the eyestalks are gradually lowered to their normal reclining position. As the crab is tilted backward and upward the eyestalks move outward and come finally to describe a 45° angle with the sagittal plane of the body; in this position the eyestalks are farthest removed from the depressed position. This movement serves to bring the best visual surface, the lateral area (B), into a position to perceive in a horizontal forward direction; whereas, when the animal is held so that the longitudinal axis is parallel to the horizontal substrate, this lateral faceted region is directed laterally. Through the employment of this rotary compensatory movement, the crab assumes an oblique position as it attains the top of a rock with steep sides; the dactyls of the ambulatory legs of the advancing side are anchored on the top edge, while the legs on the downhill side are placed just below the top of the rock. Hence, the crab is oriented to facilitate a survey of the upper rock surface with the advance eye before exposing the entire body from above. Particularly successful observations of this behavior pattern are encountered by approaching the rocky shore without undue disturbance. Crabs, previously located on the top surface, will crawl over the edge of a rock and leave visible to the observer only the dactyls and propodus of the ambulatory legs of one side, as though they were hanging from the top of the rock. By approaching with caution, following the initial disturbance of the animals on the upper rock surface, the crabs may be seen clinging to the edge of the rock in a position to observe movements on its top surface. There is little doubt that these compensatory movements contribute considerably to more successful vision which is, of course, closely associated with the general welfare of the animals in their comparatively precarious surroundings.

Repeated attempts were made to induce compensatory movements of the eyestalks by moving objects of several colors and sizes in arcs at varying distances in many planes, but all met with failure. It is difficult to comprehend this lack of eye rotation inasmuch as it transcends the supposition that rotation of the eyes serves to achieve acuteness in perception. In most vertebrate animals similar experiments are successful in inducing compensatory rotation.

Upon tilting a crab to the right from its normal horizontal position, the left or upper eye becomes lodged in its groove as if completely withdrawn; and the right or lower eye moves to an erect position almost perpendicular to the carapace. The reverse behavior is characteristic when animals are tilted to the left. Crabs observed on steep rock walls in a normal sideways orientation display this differential eyestalk movement; the upper eye is depressed, directing the anterior surface laterally and the lateral, well-faceted surface posteriorly. The lower, erect eyestalk commands a better view than if it were in its normal position. Its position provides increased posterior vision without decreasing anterior vision to any appreciable extent, while the lateral vision remains normal. The compensatory reaction suggests an adaptation to increase posterior vision when the animal's back is not to the wall, as it were, while ascending steep rocks.

Crabs which remain motionless in shallow pools or near the edges of deeper pools characteristically have the faceted surface of the eyes protruding above the water level. Perception of objects outside the pool would, of course, be enhanced because the bending of light rays upon entering the water is thereby obviated.

Rather typical responses toward the predacious gulls are exhibited by these crabs. Throughout the observations of crabs in tide pools and the surrounding rocks, rapid movements for concealment were frequently noted. Gulls in flight close at hand were the stimulating agent. On several occasions the shadow of a flying gull was sufficient to elicit a hiding response. Whether or not these responses to shadows were effected by the actual sight of

the gulls, the sudden change in light intensity, or a combination of both, is of interest. To test the effect of moving shadow alone, the writer undertook to cast shadows over the crabs from a place of concealment. The animals became startled but rarely concealed themselves in the near-by crevices. It would seem, therefore, that perception of the gulls themselves, rather than the casting of the shadows, was the stimulus contributing to the concealment response.

Several isolated observations seem to substantiate further the keen perception of *P. crassipes*. The following excerpts from my field notes will serve to describe visual acuity in this species:

The sardine, which was placed near a crevice into which a crab had withdrawn, drew several flies, one of which settled at the entrance to the crevice; the crab moved very slowly toward the fly, as if to stalk it. When within 3 inches of the fly, the crab, with a very rapid thrust of the right cheliped, succeeded in capturing the fly. A series of quick movements of the chela followed as if an attempt were being made to kill the insect; the fly was subsequently conveyed to the mouth and eaten.

This activity occurred just 2 feet below my observation post which was a collapsible blind utilized to facilitate close-up observation. Its construction consisted of a detachable frame and large-mesh wire netting through which fronds of algae were woven.

A second observation further substantiates the visual ability suggested above.

A crab was seen to emerge from a tide pool and rapidly pursue a rock slater (*Ligia occidentalis* Dana) which had ventured close to the edge of the pool. The crab had apparently perceived its objective prior to its emergence from the pool because it moved slowly out of the pool, and walked cautiously toward the rock slater. The crab did not alter its stalking pace until the rock slater took flight. Both prey and predator ran with extreme rapidity in and out of crevices in the rock wall before the rock slater succeeded in eluding the crab.

The constant behavior pattern of *P. crassipes* in response to food and materials tossed into tide pools and near uncovered ledges under which crabs were concealed has provided the basis for some simple experiments which were designed to diagnose partially the relative significance of the three senses involved in the procurement of food. Before outlining the experiments and discussing the data derived therefrom, a preliminary account of the behavior of this crab in response to food, as recorded in field observations, will be helpful in setting forth the objectives of the experiments to follow.

Without exception, providing all the animals involved were present, the initial response to food materials tossed into a middle high tide pool along the central California coast was made by sculpins (*Oligocottus maculosus* Jordan). Hermit crabs followed closely behind the sculpins. Upon rare occasions small *P. crassipes* would reach the food before the hermit crabs. It was frequently observed that food thrown into a pool failed to attract the attention of the crabs unless it was first located by other species.

The response of *P. crassipes* to floating food was rather constant. The following is an excerpt from my field notes:

A fragment of cantaloupe tossed into a pool containing *P. crassipes* within submerged crevices elicited no response until the breeze had forced the morsel toward the edge of the pool, at which time a crab emerged and walked along the bottom of the pool directly below the food. As the food reached the water's edge the crab climbed toward it, seized it with a cheliped, and pulled it to the bottom of the pool.

Similar responses were noted regularly. It is significant that the food was constantly moving, and that the crabs at no time offered to swim to the surface to grasp it.

Food tossed near exposed crevices which sheltered crabs was found soon after it fell. In one instance a crushed black turban snail (*Tegula funebralis* Adams) was tossed on a rock surface approximately 1 foot from a sequestered crab. The crab moved out, seized the turban, and returned to its crevice in 5 seconds. This behavior pattern, because of the

rapidity with which the activity occurred, demonstrates with certainty that visual perception was employed. Indeed, an identical response could be induced by tossing pebbles near the edge of the crevice; the crabs emerged, touched the pebbles with the advanced ambulatory legs, but failed to pick them up. Response time varied from 5 to 30 seconds, and on no occasion was any substance ignored.

Food lying on the rocks failed to attract the crab's attention, providing accidental contact was not made. One crab reached its crevice high on the rocks subsequent to the deposition of an odorous sardine within 3 inches of the refuge opening. A second crab emerged from the pool and passed within 6 inches of the sardine but ignored it completely. The age of the sardine provided no adverse effect upon its palatability because it was located and eaten during the extensive nocturnal wanderings characteristic of this species.

The retarded response of *P. crassipes* toward securing food placed in the tide pools suggests that this species often depends upon the visual stimulation provided by feeding activity of other tide-pool residents. To test this suggestion, observations were made in a pool which harbored no forms other than *P. crassipes.* Food materials were cautiously introduced into the pool with the aid of a long pole manipulated from behind the blind. The interval which elapsed between the introduction of the food and the initial response toward obtaining it was indicative of the proclivity of the crabs toward recognizing its presence. Between 7 and 8 minutes elapsed before emergence of the smaller crabs from crevices to seek the food. After discovery, frequent combats occurred. The larger crabs appeared soon after the smaller ones had located the food. It would seem that the movements of the smaller crabs played a rôle in stimulating the larger individuals to seek the food material.

Activity mediated chiefly through chemical stimulation was manifest on several occasions. During one observation period several fragments of abalone (*Haliotis rufescens* Swainson) were carefully placed in one end of a tide pool in which crab activity was slight. After 7 minutes the food was removed. Apparently no crabs had observed its deposition, inasmuch as no investigational activity ensued. Shortly thereafter, several small crabs left their crevices and began what simulated a random search. Shortly after the emergence of small crabs, larger individuals ventured forth. Within a short time most of the crab population of the pool was concentrated in the recently baited end. The high degree of pugnacity demonstrated by larger crabs seemed to indicate that they were perhaps strongly stimulated by the meat juices diffusing through the water of the pool. All crabs meticulously examined the substrate with the distal portion of the dactyls. Moreover, all individuals exhibited extreme complacency when the writer approached sufficiently to obtain close-up photographs of the group. Under normal conditions the similar approach of a person would instantly send them deep into their refuge places. It seemed that the stimulus to search for the origin of the meat juices superseded the natural behavior of concealment upon the approach of possible danger.

The foregoing field observations suggest that the chemical sense is ineffective in inducing rapid responses, inasmuch as the animals neglected to search for the food until it had been present for several minutes. However, it seems likewise apparent that upon adequate chemical stimulation, the chemical sense is of considerable significance in regulating the activity of the crabs. It has been suggested above that moving food, food being eaten by other individuals, or food tossed sufficiently close to a crab to stimulate its visual centers elicits an immediate response. It would, therefore, seem that the procurance of food, both in and out of water, is mediated primarily through visual stimuli.

These field data seem contrary to those set forth by Nagel (1894) and Bethe (1896, 1897) for *C. maenas.* Both authors concur that this species, in its search for food, is aided by the chemical sense; Bethe infers that the chemical stimuli are the principal ones involved, the

eyes contributing little or nothing to food procurement. Therefore the experiments outlined below were devised to test more specifically the relative utilization of the three senses in the normal habitat.

Experiment 1: A fragment of abalone viscera was wrapped in several layers of cheesecloth to make it invisible to the crabs, yet to provide ample opportunity for the diffusion of meat juices through the water. Care was taken to keep the outside of the parcel free from meat juice. The parcel was secured by a string and lowered into the pool with a long pole. A small crab, originally 8 inches from the parcel, moved to it in 30 seconds. It picked at the cloth for 25 seconds and returned to its refuge. Eight minutes later a second and larger crab visited the parcel. Shortly thereafter several other large crabs reached the vicinity of the parcel. Increased activity followed, climaxed by periodic boxing contests (see p. 180). One large crab approached the parcel, turned around, and backed up to it with the fifth pereiopods extended in a tactile-like manner. After a few seconds the crab walked away from the parcel and repeated the backing-up procedure. The parcel was pulled about the pool by the large crabs, which alternately fought their competitors and examined the bait for a period of 20 minutes before its removal from the pool.

The foregoing experiment was repeated with a rock substituted for the meat and wrapped as before. A small crab reached the parcel in 5 seconds, gave it a cursory examination and soon departed. Another approached the parcel 70 seconds later, climbed upon it to examine the surface with the dactyls, but soon moved away. A third crab arrived shortly thereafter, pinched the parcel, and left it in 4 seconds. During the remaining 15-minute interval no other crabs came to the parcel.

After the parcel containing the stone was removed, another parcel containing abalone viscera was introduced. It was significant to note that the first small crab reached the parcel after 1 minute had elapsed. This individual pinched the parcel a single time and immediately departed. Within the first 7 minutes three crabs reached the parcel but left after a hasty examination. Shortly thereafter, a large individual approached, backed up to the parcel, and meticulously examined it with the dactyls of the fifth pereiopods. Several more crabs approached, examined the parcel, and engaged in frequent contests; but they notably seized each lull in the fighting to examine the parcel further. Considerable milling about with frequent tugging at the parcel ensued for the remainder of the 15-minute period.

Experiment 2: A parcel containing abalone viscera, similar to that of the preceding experiment, was lowered upon the rocks bordering a tide pool. Although the parcel was within the usual range of many crabs, only two approached it; these abandoned it after a cursory examination. Other crabs walked close by, but none attempted to investigate the parcel in a 15-minute period.

The above procedure was repeated with a rock substituted for the meat. The parcel was placed near several crabs on the rocks but all ignored it. After 3 minutes a small crab approached it, and after 6 minutes a larger individual reached the parcel; however, both retreated after a hasty investigation. No other crabs ventured near the parcel in a 20-minute interval.

Experiment 3: A pebble smeared with abalone intestinal chyme was tossed into a pool. In 45 seconds a small crab seized the pebble in one cheliped and picked at it with the other, frequently bringing the latter appendage to the mouth. Within 30 seconds several crabs emerged and milled about the baited region. Pugnacity was intense, but the foremost activity centered on a thorough examination of the substrate with the pereiopodal dactyls and the chelae.

The procedure was repeated, with a clean pebble substituted for the smeared one. In 10 seconds a small crab located the pebble but abandoned it almost immediately. No further activity occurred near the second pebble for a 15-minute period.

Experiment 4: An abalone fragment was tossed into a pool. The splash stimulated the crabs to seek refuge. None responded positively to the food for 5½ minutes until a large crab emerged slowly from a near-by refuge and traveled in the general direction of the meat. The animal seemed to grope its way toward the meat in a manner which suggested the reception of chemical rather than visual stimuli. After this crab discovered the meat and removed it, several others congregated at the baited region and milled about it. The substrate was meticulously examined with the tips of the chelae which were frequently elevated and drawn to the mouth, thereby exhibiting evidence of strong stimulation by the juices in the water.

The same procedure was repeated but the abalone meat was first immersed in CS_2. After 30 seconds had elapsed, a crab seized the bait, conveyed it out of the pool to a position on the rock wall, and devoured it as readily as normal flesh.

Experiment 5: A fragment of abalone was tossed onto the rocks within sight of four crabs. The meat was seized by one individual in 55 seconds.

The same procedure was repeated with a piece of abalone previously immersed in CS_2. It was tossed

onto a rock 6 inches from a crab; the crab seemed frightened and returned to the water, completely ignoring the meat. However, 4 minutes later, the crab returned, seized the meat, and readily devoured it.

Other pieces of abalone saturated with CS_2 were tossed near crabs on a dry ledge. On each occasion the fragments were eaten in a normal manner. Moreover, one crab conveyed a fragment of abalone into the blind employed for these observations, an act which provided an unusual opportunity to test the reaction of the crab to odors registered as repugnant by humans. Carbon bisulphide was actually poured over this piece of meat as the crab ate it; the crab at no time exhibited any visible sign of adverse stimulation.

Experiment 6: The eyes of two large crabs were covered with a mixture of shellac, lampblack, and plaster of Paris. Subsequent to the application of this paint, the crabs would not react to shadows or movements. One crab was allowed to wander over the rocks until it remained stationary in a suitable crevice. A fragment of pungent abalone viscera was held within 1 centimeter of the oral field for 3 minutes. No response whatsoever was elicited. No antennal movement occurred although Bethe (1896, 1897) noted movement under similar circumstances for *C. maenas*; antennal movement occurs when the identical procedure is followed with *P. crassipes* immersed in water (see below). The meat was immediately grasped if it was brought into contact with the chelae. When it touched the dactyl of the second ambulatory leg, it was thrust under the body to the chelae and subsequently eaten.

The above experiment suggests that this species apparently does not react to odors. However, upon contact of the chelae and dactyls with the meat, the manipulation of the morsel into eating position was rapid. Whether or not the fleshy consistency of the food provided the correct stimulus for this behavior cannot be irrevocably demonstrated; however, some clarification was effected in a later experiment.

The identical procedure was repeated with a blinded crab in an aquarium. Whenever crabs are submerged, the antennules, antennae, and oral appendages move continually. It was necessary, therefore, to note the increase in movement of one or all of these structures to ascertain whether or not a response was elicited from an introduced stimulus. A fragment of abalone intestine was held 4 inches from the posterior end of the crab. After 15 seconds the antennules, antennae, and chelipeds moved far more rapidly than normally, registering stimulation by the food. The water was changed, and a new piece of meat was held 1 inch from the posterior end; increased appendicular movements were noted in 10 seconds. This procedure was repeated with the meat suspended immediately above the carpus of the ambulatory legs; a response was noted in 15 seconds. The procedure was again repeated with the meat suspended 1 inch in front of the oral area; a response was noted after 45 seconds.

It is apparent that the direction of the respiratory current is responsible for the differential response to the food. The respiratory current enters the branchial chamber laterally and leaves it anteriorly via a trough, thereby conveying chemical stimuli to the receptors on the antennules as the current emerges from the respiratory chamber. These facts would seem to clarify, in part, the factors underlying the backward approach to food sought by these crabs, inasmuch as detection of food via chemical means is accomplished more rapidly from the lateral or posterior than from the anterior areas.

Experiment 7: Ten blinded crabs were placed in individual aquaria; a fragment of art gum eraser was placed in contact with the dactyl of the second ambulatory leg of each. The second walking leg was employed here not only because it is the longest, but because field observations indicated that it was the one most frequently utilized by the crabs to test objects immediately below them. The crabs gathered the bits of eraser beneath them, grasped the fragments with the chelae, and conveyed them to the oral area, whereupon they were immediately rejected.

The above procedure was repeated with a small clean pebble substituted for the eraser. The pebble was completely disregarded in all cases; the animals exhibited a slightly disturbed response and moved an inch or two away from the pebble.

The experiment was again repeated, with pieces of liver substituted for the pebbles. The gathering response was similar to that shown the eraser, but the liver was eaten after it had been conveyed to the mouth.

Although the above experiments are not conclusive, they do supplement characteristic field behaviorisms which aid in affixing a partial evaluation of the comparative utility of the senses in the procurement of food. It is apparent that all three senses are employed; moreover, the degree of individual participation of the senses seems to depend entirely upon the conditions which prevail at any given time. Vision was definitely relied upon in portions of all experiments except where the eyes were rendered opaque. Visual response to food stimuli seemed apparent early in each experiment, which implies that movement of the food material was significant. Instantaneous response to food materials some distance away can be regarded

as depending entirely upon visual stimuli, because without exception the diffusion of food juices through the water required several minutes (Experiments 1, 3, 4, and 6). Furthermore, it seems, from Experiments 1, 3, 4, and 6, that the threshold of chemical stimulation for this species is relatively high because responses which suggested stimuli of chemical nature were invariably delayed several minutes after the introduction into the pool of some food substance. In Experiment 6 the juices were visible in the water about the crab for several seconds before response was shown.

The tactile sense of this species appears to be rather highly developed. Except in Experiment 5, the participation of this sense was clearly revealed. The apparent prodding by the chelae and distal podomeres of the remaining pereiopods discloses that these crabs rely greatly upon this sense in their food procurement. Moreover, it is employed equally well in and out of water. In addition to explaining the frequently observed backward approach to food under water on the basis of the orientation of the respiratory current, the elevation of the fifth pereiopods to be employed as testing structures brings forth the supporting rôle played by the tactile receptors. It is significant to note that this backward approach to food has never been observed out of water, suggesting that in this type of reaction under submerged conditions, tactile sensations are subordinate to chemical ones. The data derived in Experiments 6 and 7 provide proof that food is identified by the dactyls, although the latter experiment seems to indicate that these structures are not selective chemically. Experiment 7 provides evidence that the dactyls do distinguish texture of substances; and inasmuch as their chemical reception is slight or wanting, the major rôle played by the dactyls in food procurement may possibly be concerned with texture differentiation. Food materials may be selected in this manner because they feel soft and fleshy. At any rate, the spongy texture of the art gum eraser was sufficient to release all the reactions attendant to food manipulation.

Nocturnal foraging, the chief type involved in food procurement by this species, presents an entirely different aspect of comparative sensory participation. Apparently vision is completely in disuse at this time. Motion near crabs at night elicits no response; however, if the moving object is slightly illuminated, instantaneous responses occur. Furthermore, the nocturnal behavior of this species tends to limit the utility of the chemical sense because the crabs emerge from the tide pools and forage high on the rock surfaces. Experiments 2, 5, and 6 indicate that odors elicit virtually no response; consequently, the chemical sense is reduced to the sense of taste alone, which would seem to serve no significant function in the actual searching for food.

The tactile sense becomes exceedingly important at night in lieu of the non-effective visual and chemical senses. Inasmuch as the major constituent of the diet is algae, primarily of the ulvaceous type, and since the foraging area is generally adjacent to diurnal refuges, the tactile sense apparently meets the requirement of food procurement. Fishermen frequently leave sardines and other bait materials high on the rocks upon the termination of their activities. These food caches are frequently located during the nocturnal wandering of the crabs, notwithstanding the fact that this food is often deposited in supralittoral areas which are several feet higher than the normal upper horizon of the diurnal range. Frequently, too, these food caches are unnoticed although crabs often wander near them. It seems reasonable to assume that those found were located accidentally, rather than through the medium of a sense of smell.

Additional information concerning the tactile sense was derived through observations on normal and blinded animals. Two crabs, one with opaqued eyes and one in a normal condition, were released on a rock 1½ feet from the edge of a tide pool; the rock sloped gently to the pool. The normal individual ran rapidly to the water, submerged, and concealed itself under a rock. The blinded crab wandered slowly

and aimlessly about the rock surface, going directly away from the water at the start. As it walked along, the advancing ambulatory legs were held out straight from the body when not employed for support. After 10 minutes of this slow, groping ambulation, the animal reached the water's edge. Upon entering the pool the crab passed over the algal film at the edge and immediately proceeded to forage by scraping it with the tips of the chelae, exactly as normal crabs would do.

Two additional blinded crabs were released at the locus mentioned above. One groped about the rock, settling momentarily in any shallow, sun-swept crevice encountered, but finally established itself in a larger crevice 1 hour after its wanderings had begun. At this time it was but 5½ feet from the point of release. The second crab paralleled the activity of the first but soon became oriented in a direction leading to the pool. The advancing pereiopods were employed as tactile structures. After the crab entered the pool, it descended along a ledge with the fifth pereiopods held high upon a perpendicular wall and walked with the remaining three pairs. The advancing appendages were alternately utilized for support and tactile organs. The chelae were elevated and spread at a wide angle, apparently to provide defense for any exigency. The foregoing observations seem to indicate that although the eyes are the chief means of orientation, tactile perception can be substituted although with considerable forfeiture of efficiency.

Notwithstanding the rather high development of the tactile sense, this species apparently does not hear sounds within the human range of perception. Crabs only 5 feet away from the blind exhibited no response to noises made by shouting, clapping hands, or the pounding together of rocks. Moreover, loud shouting at night within 2 feet of foraging individuals failed to elicit a response. Further observations pertaining to the rôle played by the various senses are incidental to the main theme of certain other aspects of this study and will be set forth where pertinent.

Diurnal and Nocturnal Distribution

Throughout the diurnal hours, members of this species tend to remain secluded in crevices, regardless of their position in or out of tide pools. If undisturbed, they may wander about in the tide pools or over short distances on the rocks. At the first sign of danger they dash into crevices and often literally fall down the rocks to conceal themselves in the deep crevices below.

The movement from the refuges to the higher rock surfaces begins after dusk at a time when artificial light is required to observe the crabs. Many crabs align themselves along the edges of the tide pools to scrape the algal mat. Others climb high on the rocks in search of the rich supply of minute algae which grows within the splash zone. It is a rare occurrence to find a crab concealed in a crevice at night unless some disturbance has stimulated it to seek refuge. Artificial illumination does not disturb their foraging habits. However, if motion occurs in close proximity to them in the presence of faint illumination, they will move rapidly toward the protective crevices. Virtually all the collections which have provided data for this study were made during the night, because a true representation of sizes and intermolt stages in the population could be obtained only at this time. The observed night population is many times greater than that observed throughout diurnal periods.

This species is not unique in its nocturnal habits. Bateson (1889) states that most Crustacea are more active by night than by day, while Hara (1933) reports that the land crabs, *Varuna literata* and *Sesarma tetragonum*, are considerably more active at night. Drezwina (1908), while studying phototropic response in *Pachygrapsus marmoratus* and *C. maenas*, found that *P. marmoratus* invariably chose the darkened end of an aquarium, while *C. maenas* preferred the illuminated end.

P. crassipes was found to prefer the darkened end of an aquarium if the water was constant in depth throughout the darkened and illuminated halves. When an aquarium was tilted to

provide deeper water at one end and none at the other, this species preferred the deep end regardless of its darkened or illuminated character. The foregoing data, secured from dozens of laboratory animals reared over a period of 3 years, suggest that although this species is negatively phototropic, the hydrotropic responses are dominant.

Locomotion

Locomotion of Brachyura has been investigated by List (1897), Bethe (1897), and Cowles (1908). The initial two workers confined their studies to those species which are essentially restricted to an aquatic life and are not particularly adapted to locomotion on land. Cowles, on the other hand, limited his observations to *Ocypoda arenaria,* a land crab which travels with relatively great speed. The present data for *P. crassipes* describe locomotion in an animal which is neither strictly aquatic nor essentially terrestrial, but which occurs on the strand in a position between those types previously investigated. Bethe (1897) observed that *C. maenas* ordinarily travels sideways, but that to a very limited extent it can move forward and backward; in any event, he does not concur with List (1897) that Brachyura, in general, travel in an oblique direction.

Like *C. maenas, P. crassipes* normally runs and walks in a direction perpendicular to the sagittal plane of the body. It is not unusual, however, for the crabs to travel in other directions. Unlike *C. maenas, P. crassipes* moves obliquely sideways with little decrease in speed and travels directly forward with ease. It has been previously stated that this species can move backward when approaching food in a tide pool or when backing into a refuge. When speed is mandatory, the movement is invariably sideways; but when foraging is the chief objective, the crabs can and do move in any direction. Pugnacious crabs have been observed to approach each other by walking directly forward for distances up to 2 feet. The chelae are flexed in front of the oral area during the approach to combat.

The sequence of movement of the ambulatory legs is 2, 3, 1, and 4. Often, however, the third and first legs move concurrently. Variations occur in the sequence of movement, but the order mentioned above is invariably adhered to during normal walking. It is significant that the second ambulatory leg, which is the largest, initiates movement; its length probably permits it to be utilized both as an ambulatory and tactile organ.

Crabs taken by surprise when the rocks under which they are concealed are overturned, resort to speed and skillful dodging to escape capture. The ease with which they move in any direction is exceedingly advantageous. Under no circumstances do they feign death, a behavior pattern characteristic of the closely associated *H. nudus.* It is a general hypothesis that crabs achieve greater agility and speed as they become adapted to exposed conditions. For example, members of the land-crab genus *Sesarma* have been estimated to run approximately 10 miles per hour; whereas *C. magister,* an aquatic species, is exceedingly sluggish on land. A study of the speed of *P. crassipes* was considered significant because of the unique transitory position of this crab between the littoral and terrestrial areas. Although an accurate speed test for *P. crassipes* is difficult to make, several large crabs were placed on the starting line of a course laid out on a flat rock. Each crab was frightened and caused to run while a stop watch was employed to record the times involved. Many resorted to dodging tactics, but the writer was successful in obtaining some time records over very short distances. The distances involved were too short to provide accuracy, but an indication of the possible speed of movement was obtained. The most rapid time clocked was 0.9 second over a 4-foot course, indicating a speed of approximately 3 miles per hour. For all practical purposes this speed seemed to coincide with field estimates of speed. Therefore, *P. crassipes* runs approximately a third as rapidly as *Sesarma.* Despite the comparative slowness of *P. crassipes* in contrast to *Sesarma,* additional

evidence for the hypothesis set forth above for brachyurans concerning the correlation of speed with habitat may be obtained by comparing the speed of the former with that of its more sluggish, near relative, *H. nudus,* located at a lower level on the strand.

Swimming is rarely undertaken by *P. crassipes* and is poorly executed because of the lack of structural adaptation for this method of locomotion. Infrequently, crabs were observed to leave the top of a submerged rock by giving a powerful kick; the ambulatory appendages then move at a very rapid rate until the animal attains the opposite bank. At no time has swimming been successfully undertaken over distances in excess of 1 to 2 feet. Movement through the water is retarded, notwithstanding the fact that the appendages are moved swiftly. On one occasion a crab swam forward by moving the limbs in an anteroposterior direction instead of the normal lateral flexing. This method seemed more efficient than the usual lateral swimming because the broad surfaces of the legs provided greater resistance to the water.

Food and Feeding Habits

The food of *P. crassipes* consists, in order of decreasing importance, of (1) live algae, both matted and frondal, (2) detritus left by receding tides and fishermen, and (3) living littoral animals.

By far the most important method of food procurement is the scraping of the minute algal mat from the bottom and sides of tide pools, damp crevices, and the tops and sides of boulders. The excavated tips of the chelae (Fig. 3) are highly adapted to this method of foraging. The algae most commonly eaten are listed on page 141.

Nocturnal foraging is preferred and large numbers of crabs are found at night high on the rocks in the splash zone where they scrape the algal film. Nocturnal foraging is not peculiar to *P. crassipes* and seems to be prevalent among Brachyura in general; most land crabs (Cowles, 1908; Andrews, 1909; Cott, 1929; Hara, 1933), some spider crabs (Milligan, 1915), and undoubtedly many others are more active nocturnally. Diurnal feeding, however, is common with *P. crassipes,* particularly on warm days. The crabs do not venture far from the pools or refuges, and are content to forage on the algal film growing adjacent to their places of concealment. When the tide recedes, they frequently engage in consuming the short fronds of *Ulva* which cover the boulders in many areas of the strand.

The lack of pugnacity among these comparatively belligerent animals during their foraging on live algal food seems to indicate that intraspecific competition for this type of subsistence is negligible. It has been mentioned previously that crabs frequently appear to be so completely absorbed with foraging activities that they are unaware of approaching danger from predators.

Other workers who have recorded observations on this species (Hewatt, 1936; Ricketts and Calvin, 1939) have placed emphasis on detritus as the principal source of nutriment. Inasmuch as their observations were divided among all the littoral forms and perhaps directed toward these crabs only at infrequent intervals, it is probable that they were impressed with this type of food material which seems, from far more extensive study, to be secondary in importance. While it is true, as Ricketts and Calvin (1939) state, that these crabs and the beach hoppers are the most active scavengers in this particular ecological association, it is evident from the information at hand that food secured from this source contributes but a minor portion of the total diet. All available carrion is quickly consumed, but the amount of carrion deposited on the rocks by the receding tide is almost negligible; indeed, observations of crabs eating food of this nature are infrequent.

The least significant food source (Pearse, 1931, to the contrary), but the most interesting from the point of view of behavior, is other littoral animals. Variations as to the extent and type of predacious behavior were disclosed among crabs in a given locality as well as be-

tween widely separated populations. A single record of a most interesting behavior pattern was taken during observations on crabs in a tide pool at Moss Beach, California. The following excerpt from my field notes serves to describe this activity.

A large male walked slowly by a black turban (*Tegula funebralis*) in a forward direction; it stopped beside the turban, quickly side-stepped laterally and grasped the shell, overturned it, and seized the turban behind the operculum with a cheliped before it could withdraw. The crab held the turban for several minutes, making repeated attempts to pull it from its shell. After attempts to extricate the animal met with failure, the free cheliped was employed to tear the flesh behind the operculum. A few seconds later the crab repeated its stalking behavior on a hermit crab in a black turban shell, but the hermit crab withdrew before the crab could grasp it. The opercular function of the hermit crab's large cheliped was dynamically illustrated.

Observations made along the Monterey coast disclosed repeated attempts by *P. crassipes* to crush the shells of the littorines which are present in vast numbers in the high-tide pools. All attempts met with failure. Recently molted, partially devoured *H. nudus* were found in two tide pools at Monterey. Circumstantial evidence seemed to incriminate *P. crassipes* inasmuch as it was the predominant inhabitant of the pools, particularly since it is known that it is cannibalistic on recently molted individuals.

Indisputable records of cannibalistic behavior in this species—17 in the laboratory and 3 in the field—were secured. The soft parts of the body are eaten; the pereiopods and branchial chambers are undisturbed. Without exception, the ravaged individuals were recently molted animals, no later than stage A_1. Recently molted animals in the laboratory aquaria were invariably victims, if hard crabs were present in the same aquarium. It was early discovered that molt and intermolt data had to be secured from isolated individuals in the laboratory. The lack of more frequent records of cannibalism is undoubtedly correlated with nocturnal ecdysis and the rocky habitats with abundant refuges to which the crabs retire immediately after exuviation.

Stomach analyses were made on 50 specimens of this species collected early in the morning. The crabs were preserved in 10 per cent formalin and examined shortly thereafter. The major constituents detected in order of decreasing quantity were as follows: algal tissues, diatoms, and striated muscle fragments. The latter item was found in 17 stomachs; several partially devoured sardines left adjacent to the pool by fishermen were undoubtedly the source. Had the fish been absent, it is doubtful that any animal food would have been found in the stomachs. These data serve to substantiate the field observations presented above. Pearse (1931) cites food consumption figures of 51 per cent flesh and 49 per cent plant material for *P. crassipes* in Japan. If these data are normal, the food habits of the Japanese representatives differ widely from those on the American coast.

P. crassipes along the central California coast may be designated as essentially an herbivore, ordinarily a grazing herbivore, less commonly a plant scavenger, while facultatively a carnivore, chiefly an animal scavenger, and less frequently a predator. An organism subscribing to such generalized food habits can easily withstand periodic deficiencies in one or more food sources; this, coupled with the fact that the high littoral zone offers an uncontested food supply, has been a major factor underlying the success of this species.

Use of the Chelipeds

The chelae are perhaps the most important and useful appendages of *P. crassipes*, and as such merit special consideration here. The several podomeres articulate at varying angles, enabling the crab to describe an extensive arc about itself. Sexual dimorphism with respect to the chelae is negligible, those of the male being only slightly larger. Although very few of the normal activities of this crab are ordinarily undertaken without the use of the chelae, several crabs which had autotomized the chelae

were observed both in the laboratory and field to be undertaking the necessary activities without the use of these appendages. Under these circumstances the first pair of ambulatory appendages was utilized to perform several of the duties usually identified with the chelae. The duties of these appendages are varied but their major accomplishments are food procurement and protection, with reproductive activities associated with them to a lesser extent.

Food procurement is achieved in several ways with the aid of these structures. The spaded tips are adapted for scraping the algal mat; the toothed inner borders of both the dactylus and finger of the propodus are employed to hold and tear flesh and algal fronds. Upon discovery, fleshy food is invariably grasped by the chelae and conveyed to the oral region. Two methods of employing the chelae during scavenging were commonly observed: (1) one cheliped holds the material while the other conveys bits of it to the mouth; (2) both chelae hold the food in juxtaposition to the mouth parts while the mandibles chew off bits from the periphery of the food material. When the latter method is employed on a disc-shaped fragment of flesh or algal frond, the bites of the mandibles produce a scalloped pattern on the periphery of the food item.

It was commonly observed that crabs dragged their food out of the tide pools to higher sections of the rocks. Frequently, other crabs would contest the food and a veritable tug of war would ensue, each animal grasping the food with one or both chelae.

In addition to the prehensile use of the chelae, this species apparently employs them to aid in food selection. Crabs which slowly walk over the substrate often drag the chelae and frequently halt to scrape the substrate with one or both of these appendages. An examination of the setae on the propodus and dactylus reveals the presence of both the long and the short type of setae, which suggests that both tactile and chemical stimuli are perceived. At least one other crab is said to utilize the chelae in the selection of food (Pearse, 1912). There is little doubt that the chelae of *P. crassipes* have functional tactile receptors, but observations fail to establish any clue concerning their capacity to function for chemical perception.

Both chelae are employed with equal facility in conveying food to the mouth when they are identical, or nearly so, in length. Observations were made on five crabs for periods ranging from 2 to 16 minutes to ascertain the number of movements of each cheliped per minute. No consistent preference was shown for either cheliped by these crabs; and out of a total of 626 movements by all five crabs, 320 were made by the right cheliped, while 306 were made by the left cheliped.

The use of either cheliped in securing fragments of *Mytilus* on a shell apparently depends upon the side from which the food material is most easily taken. One cheliped is employed to hold the shell, the other is utilized to tear the flesh and convey it to the mouth. However, exceptions were apparent in those animals which had recently regenerated an undersized cheliped. Invariably, the food was held with the large cheliped, while the flesh was torn away and conveyed to the mouth by the diminutive one, a unilateral type of feeding which is characteristic of male fiddler crabs (Pearse, 1912; Schwartz and Safir, 1915). The pugnacity of *P. crassipes* is shown through the activity of the chelae. A substantial portion of the diurnal activity of this species is concerned with frequent clashes between individuals of the same and opposite sexes, with combats between males predominant. If the combatants differ markedly in size, the larger crab usually displays little interest in the contest and soon wanders off, even though he may be hotly pursued by his smaller antagonist.

During a contest the crabs face each other and frequently box with flexed chelae by pushing at the antagonist's chelae with the flattened external surfaces. If this activity fails to result in the retreat of one combatant, the chelae are extended and rapid thrusts are directed at the opposing crab. If the contest is between two males of comparable size, the thrusting of chelae

may continue for several seconds; one of the crabs usually withdraws from the contest. The proximity of food accentuates the pugnacity, and contests occur among all sizes and sexes. Crabs of this species have never been observed to lock their chelae on their adversaries in any manner, although it seems likely that this behavior might occur as it does in the fiddler crabs (Pearse, 1912). These conflicts, although frequent, result in little if any dismemberment of individuals; no casualties have been observed, although innumerable contests have been witnessed.

Defense against predacious enemies is accomplished both by flight and by action of the chelae. The latter behavior is manifest when the crabs are picked up; the chelae provide vigorous opposition to predators through their strong, vise-like grip. In addition to pinching action, the articulation between podomeres enables the cheliped to undergo considerable torsion, contributing greatly to the discomfort of the predator.

Crabs which have been cornered by an adversary take a stance designated by Bethe (1897) as the "Aufbaumreflex." The animal elevates itself upon the dactyls; the chelae are raised and spread widely; and the body proper is held well above the substrate. This behavior is primarily a bluff to deter the antagonists, because the crab will take flight if an opportunity for concealment is at hand; however, lacking that opportunity, the defiant animal will fiercely thrust the chelae at the attacker.

Chelae seldom participate in the reproductive activity of *P. crassipes*. Throughout copulation the chelae of both sexes are generally flexed against the oral field; infrequently, those of the males assist in grasping the female. No nuptial activity is assigned to the chelae although such activity has been suggested for male fiddler crabs (Alcock, 1892). The sole indication of a nuptial activity was a slight up-and-down movement of the flexed cheliped of a male which became separated from a female during copulation.

Activity under Varied External Conditions

The diurnal activities of this species in a tide pool attain a maximum intensity on bright, sunny days; their movements perceptibly slacken on dull and cloudy days. To place the measurement of activity on an objective basis, a record was made of the number of complete movements made by the chelae from the substrate to the mouth while the crabs were scraping the algal mat. The animals selected for observation were scraping and feeding on the algal mat immediately below the surface of the water near the perimeter of a tide pool. Temperatures were taken of the water near the crabs. Movements of the chelae of each crab were recorded over 4-minute intervals.

These data, together with extensive field observations on territorial associations, indicate that activity of the crabs is correlated with the temperature; activity seemed significantly slackened below 65° F. and accelerated when temperatures increased beyond this figure. On foggy days during which the sun was continually obscured, the temperature of the tide pools was generally lower than that of the air and crab activity within the tide pools was slight. The rapid rise of tide-pool temperature during periods when the sun is unobscured tends to benefit the crab population by providing conditions under which this species is most active.

The conspicuous inactivity of crabs under shaded ledges was in unequivocal contrast to the intense activity which occurred in adjacent tide pools. On a relatively warm day temperatures of the outside air, of air under a ledge in which crabs were concealed, and of tide-pool water were found to be 60°, 58°, and 84° F., respectively. It would seem, therefore, that this temperature differential would satisfactorily account for the differences in activity between tide-pool and under-ledge crabs. Observations which extended over several consecutive hours showed that even during the warmer days of the year the crabs under ledges exhibited only a minimum of movement.

Tide pools remained warmer than the air for the first few nocturnal hours, which accounts partially for the intense activity in the pools in the early evening. Later in the night, the crabs wandered out of the tide pools and ledges to forage areas higher on the strand. The air temperatures were, at this time, relatively low; consequently, the foraging animals moved quite slowly. The foregoing data indicate that temperature must be added to the factors which exert a regulatory effect on these crabs.

In addition to temperature changes, the periodic fluctuation of activity created by the changing tide must be considered in any discussion concerning the behavior of a littoral species. The subsistence of *P. crassipes* in the littoral zone subjects the animal to regular changes of exposure and submersion, with the result that the sum total of its activities tends to be placed on a rhythmical basis. Its elevated position on the strand has succeeded in removing some of the restrictions on activity and inactivity imposed upon species located lower in the littoral area; nevertheless, the tidal influence was clearly manifested. The relative inactivity of the crabs during high tide, and the activity shown throughout the hours of exposure, furnished evidence of a behavior pattern which seldom deviated from the standard; indeed, it tended to be stereotyped. The life of this crab seems to approach a monotony of repetitions, a seldom-changing series of actions and reactions.

The Influence of the Ocean on P. crassipes

Drezwina (1908) studied the influence of the ocean on *C. maenas* in some detail; she concluded that the crabs showed a tropic response to the sea, which she designated "hydrotropism." The wind, slope of the land, and amount of light were demonstrated to have no bearing on the response which repeatedly occurred in the same manner without regard to external conditions. None of the crabs traveled in a direction opposite to the sea, and the crabs with painted eyes oriented themselves no differently from normal ones. Time did not permit a study of these behaviorisms in great detail for *P. crassipes,* but the results of some simple field observations tend to confirm the findings of Drezwina with some modification.

Sixty-one crabs were released high on the beach behind a rocky outcrop which shielded the sea from the sight of the crabs. The writer stood 10 feet to seaward from the point of release. Many small rocks were strewn about the area, both in a direction away from the sea and toward it. Approximately one-half of the crabs immediately started toward the ocean, disregarded rock refuges in the vicinity, traveled around the rocky outcrop, and went down the inclined beach for several feet before concealing themselves in ledges situated there. After a momentary stop, most of them continued toward the water until damp crevices or small tide pools were reached. Of the remaining half, many traveled parallel to the ocean and halted momentarily at each rock encountered. Although the water was visible, several crabs traveled at least 20 feet in a lateral direction before they moved toward the ocean. The remaining crabs went away from the sea and took refuge below rocks higher on the strand, a behavior in notable contrast to that of *C. maenas* (Drezwina, 1908). In some individuals the stimulus for concealment apparently overcame the desire to seek the ocean water. Within an hour's time the crabs high on the beach gradually moved from rock to rock in a direction toward the sea. At the close of a 2-hour observation period, all had either reached the edge of the water or were secluded in moist crevices. Although the innate tendency of all crabs to react in a like manner was evident, the response was more pronounced in some individuals than it was in others. It is barely possible that some of these crabs, which were collected during the night on their high foraging area, were representatives of low tide-pool areas, while others may have chosen a higher level in the rocks as their usual habitat. Perhaps concealment in the high, dry crevices would suffice for the latter crabs, whereas the former would have a stronger tendency to seek

water. A more thorough investigation of these phenomena is required to classify the differential responses.

To test further the influence of the ocean on this species, 25 normal crabs and 25 blinded crabs were released in groups of 5 from a locus in a shallow depression atop a large rock surface which was several feet higher than the splash zone. The ocean bordered the rock on the outer and lateral sides. The air was virtually calm, and the day was bright and warm. The wanderings of the crabs for a period of 10 minutes were recorded (Figs. 13 and 14). The solid lines represent uphill travel, and the dashed lines represent downhill travel. The concentric areas delimit distances of 3, 6, and 12 feet and serve to indicate the distance traveled by the crabs. With the exception of the landward side, the ocean was approximately equidistant from the point of release.

These data show that one of the patent behaviorisms of these crabs is to seek a concealing crevice. The normal crabs immediately sought the crevices; five gradually attempted to make their way toward the ocean. The slope of the rock seemed inconsequential inasmuch as the animals did not deviate from the general direction of travel. It is significant that none of the normal crabs left crevices to travel in a direction counter to the ocean.

The data for blinded crabs compared favorably with those secured for normal ones. In

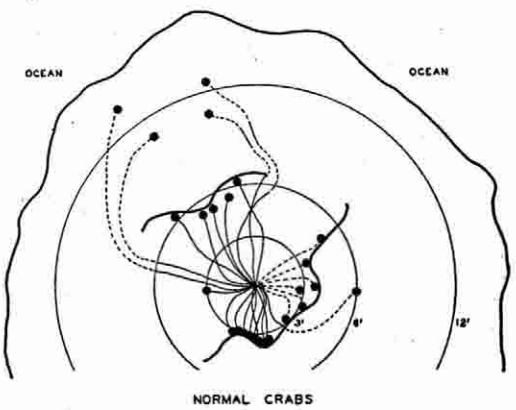


FIG. 13. The movements of normal *P. crassipes* within a 10-minute period subsequent to their release high on the rocks. (See text for details.)

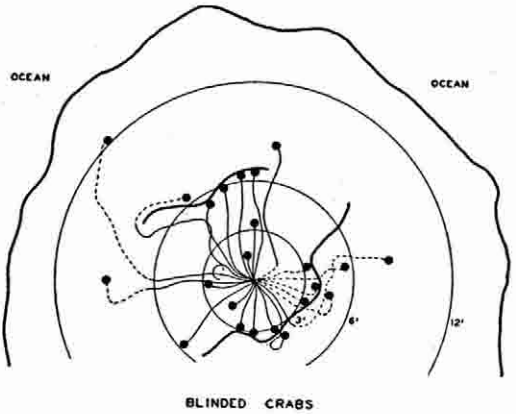


FIG. 14. The movements of blinded *P. crassipes* within a 10-minute period subsequent to their release high on the rocks. (See text for details.)

contrast to normal crabs, Figure 14 reveals that the blinded ones traveled in all directions from the locus. Moreover, they traveled in uncertain paths, frequently reversing and recrossing. Those which located crevices were content to remain. Those which walked around to the top side of the large crevices wandered about aimlessly and failed to locate a refuge. Crabs of both groups eventually traveled toward the ocean; none ventured away from it.

The response of this species toward wave action is virtually stereotyped. Its behavior is not that of extreme fear, such as Schwartz and Safir (1915) suggest for *Uca,* although it bears an overt resemblance to such behavior. The response varied slightly, depending on whether the animals were located in tide pools or in rock crevices. Upon the initial indication of wave action, crabs in a tide pool curtailed their activity to a minimum. As the wave action became more intense, the animals concealed themselves deep in their crevices, and did not emerge until the tide receded.

Crabs under ledges withdrew at the first splash of a wave, moved back as far as possible, and wedged themselves in by pressing the carapace and appendages against the rock. At no time were crabs observed in vulnerable locations as the tide approached their refuges. Crabs which had climbed up to high, less-protected areas

returned as the tide receded to the deep crevices below. The foregoing behavior pattern seems contrary to their previously mentioned penchant for remaining out of water. Crabs which follow the receding tide return as the tide ebbs and begins to rise. It seems apparent that the deep crevices just below high-tide level offer for this species the most desirable refuge against wave action.

Relationship of P. crassipes *to Certain Other Species in the High Littoral Zone*

General interrelationships with respect to the biota of the strand at Monterey Bay, California, have been set forth by Hewatt (1936). The present observations serve to supplement those recorded by Hewatt for the littoral species more or less closely associated with *P. crassipes.* Although this species is generally found in a fasciation relatively uncontested by other forms, its extensive vertical range brings it into intimate association with several other brachyurans which provide potential competition.

The association of *P. crassipes* and *H. nudus* is perhaps the most important because of the overlapping refuge places in certain regions throughout much of their geographical ranges. It has been found that a differential interspecific tolerance exists in different types of biotopes. At Monterey both species were commonly found just below high-tide level, under rocks which rest on a solid substrate, or on coarse gravel. In addition, both occurred in tide pools which lie below high-tide level. Although there was no interspecific antagonism displayed on the boulder beach, the individuals which occupied the tide pools frequently engaged in combats for certain desirable crevices. At no time were the two species found in juxtaposition. The relatively larger chelae of *H. nudus* generally enabled these crabs to drive off *P. crassipes* of comparable size.

Extensive collecting soon demonstrated that *H. nudus* remained in refuges which were lower on the strand and generally cooler than those of *P. crassipes.* Inasmuch as temperature appears to be a significant factor in the distribution of littoral animals, the temperature was recorded in the localities which seemed to contain most of each of the two species of crabs at midday. The air temperature during this investigation was 69.5° F.

Temperatures of 10 rock crevices containing *P. crassipes* ranged from 58.6° F. to 61.2° F., with a mean temperature of 60.0° F. Temperatures of the moist sand under 12 rocks harboring *H. nudus* ranged from 57.6° F. to 59.8° F., with a mean temperature of 58.0° F. Thus, the differential of temperature between the rock crevices and surface sand below rocks harboring *P. crassipes* and *H. nudus,* respectively, is slight and probably does not account for the different locations selected by each crab. Midday temperatures of eight high tide pools frequented only by *P. crassipes* ranged from 68.2° F. to 84.5° F., with a mean temperature of 72.0° F.; whereas temperatures of eight lower tide pools containing mostly *H. nudus* ranged from 56.5° F. to 59.3° F., with a mean temperature of 57.5° F. or 14.5° F. lower than the average of the higher pools. Thus, the temperatures of tide pools may have considerable influence upon the segregation of these species, *H. nudus* being as characteristic of the zone of the rockweeds (2.0 to 4.0 tide level) as *P. crassipes* is of the naked zone higher up (over 4.0 tide level). Although their zonation on the strand overlaps to some extent, very few of the individuals of one species ever have contact with those of the other.

Foods consumed by *H. nudus* and *P. crassipes* differ sufficiently to reduce to a minimum interspecific competition for sustenance. The former subsists primarily on detritus and infrequently on algal fronds; whereas members of the latter species sustain themselves on scrapings of the algal film and on detritus. During the intensive nocturnal feeding, *P. crassipes* climbs to the tops and sides of boulders to eat young *Ulva* fronds, while *H. nudus* remains below the boulders, seldom attempting to climb them. Because of dissimilar feeding habits, the association of these species within the same tide pool is not strictly competitive.

Intimate association between *P. crassipes* and *H. oregonensis* was rarely observed along the outer coast, but was frequently observed in bays and estuaries. Here, as in the association with *H. nudus,* the propinquity of the species was primarily for purposes of concealment in a habitat which provided a minimum of refuge places. In the third biotope (see p. 142) both species occupied adjacent holes in the muddy bank. On several occasions individuals of *H. oregonensis* were observed to enter holes concealing *P. crassipes.* The hasty departure of the former indicated that the two species rarely, if ever, concealed themselves within the same hole. Moreover, the holes which contained *P. crassipes* were found to have only a single occupant; those which concealed *H. oregonensis* often sheltered from one to three individuals.

Both *P. crassipes* and the porcellanid crab *Petrolisthes cinctipes* Randall are found under rocks of the upper and middle tidal zones. Undoubtedly, the concealing habits of both species are responsible for their association inasmuch as no specific, competitive interrelationship has ever been recorded. There can be no competition for food because *P. cinctipes* is a plankton feeder (MacGinitie, 1937). Associations between *P. crassipes* and several other littoral types have been discussed elsewhere in this paper.

Precocious Young

The extraordinary display of activity shown by young individuals of this species is sufficiently outstanding to merit special attention. The young of many cursorial and defenseless ungulate mammals are able to run within a short time subsequent to birth, have the legs developed out of all proportion to the body, and usually exhibit mental precocity to a marked degree. Similarly, the immature individuals of *P. crassipes* are able to attain comparatively great speed, have the legs relatively longer than the adults, and likewise exhibit a high degree of alertness. Although this species is confined to a lower littoral stratum than are the true land crabs, which exhibit all these characters on a more highly evolved level (Pearse, 1912, 1914; Cott, 1929), the long periods of exposure of *P. crassipes* seem to have provided sufficient stimuli for the manifestation of those faculties ordinarily associated with animals in less protected habitats. The eyes of young crabs seem to be comparatively larger, and the legs appear to be relatively longer than those of adult crabs. In order to check these characters, crabs of representative carapace lengths (measured from the front to the posterior border), from the first crab stage to the largest individual, were selected, and measurements of the long, second ambulatory leg and the greatest length of the faceted surface of the eye were recorded. The length of the eye was measured along the greatest (longitudinal) length of the faceted surface and does not include the eyestalk and terminal style. From these measurements ratios were computed between the length of these structures and the carapace. These data are set forth in Table 4.

TABLE 4

RATIOS BETWEEN THE LENGTH OF THE SECOND WALKING LEG AND LENGTH OF FACETED EYE-SURFACE TO LENGTH OF THE CARAPACE OF SEVERAL INDIVIDUALS OF *P. crassipes* RANGING FROM 3.3 TO 38.3 MILLIMETERS IN CARAPACE LENGTH. (MEASUREMENTS IN MM.)

CARAPACE		SECOND WALKING LEG		EYE	
Breadth	Length	Length	Ratio of Length of Leg to Length of Carapace	Length	Ratio of Length of Eye to Length of Carapace
3.7	3.3	5.0	1.82	0.76	0.23
9.1	7.6	13.3	1.75	1.3	.17
15.2	13.4	24.2	1.80	1.7	.13
20.5	17.8	30.6	1.71	1.9	.11
24.0	21.0	35.0	1.66	2.1	.10
31.1	25.9	43.6	1.68	2.4	.09
37.6	31.7	50.4	1.58	2.5	.08
45.8	38.3	61.0	1.59	2.8	0.07

It is apparent, by reference to columns 4 and 6 that the length of the second pereiopod and of the faceted surface of the eye, respectively, as compared with the length of the carapace,

is relatively greatest in the youngest crabs. Further, the ratio gradually decreases as the size of the crab increases, reaching the final and lowest value in the largest crabs.

Despite the fact that the visual perceptive surface of the eyes of small crabs is comparatively greater than that of larger crabs, we cannot conclude that their apparent precocity results from better vision. Indeed, the larger individuals, which possess considerably flatter faceted areas that enable them to direct more ommatidia toward an object, are certain to perceive objects with greater facility. Undoubtedly the precocious development of the eyes substantially contributes to the alertness of the younger individuals but their bolder habits with respect to potential danger, and their ability invariably to reach food tossed into a tide pool before the larger crabs, probably result from nervousness peculiar to young crabs, which are merely activated by visual stimuli. It is possible that their lack of experience and associated inhibitions contribute to their behavior. The older crabs seem to proceed with far more reserve and caution.

The comparative agility of young *P. crassipes* and *H. nudus* or *H. oregonensis* was well illustrated when collections were made by rapidly turning over rocks along the shore. The immature specimens of *P. crassipes* were easily segregated by turning over small rocks and grasping the most rapidly moving crabs which were invariably this species. The small, sluggish crabs under rocks were generally young *H. nudus* or *H. oregonensis.* The nimbleness characteristic of young *P. crassipes* is in marked contrast to the sluggishness of the other two species. Although the cursorial attainments of these small crabs are far less effective than those of true land crabs, young *P. crassipes* are definitely segregated behavioristically from the more phlegmatic marine forms.

Intraspecific Territoriality

Early observations on the general behavior of *P. crassipes* disclosed apparent territorial relationships among individuals in tide pools. Investigators of fossorial land crabs (Pearse, 1912; Cowles, 1908) have shown that these animals return to their burrows from distant points on the beach. The behavior was considered to represent a homing instinct rather than a territorial behavior, although Pearse states that fiddler crabs would contest the presence of any crab at the mouths of their burrows. Studies on territorialism among the Crustacea in general have been neglected, with the exception of terrestrial isopods (Allee, 1926, 1938; Miller, Ph.D. thesis in the Library of the University of California) and the littoral isopod genus *Ligia* (Miller, *op. cit.*) which achieve some degree of social aggregation. No critical investigations of territorial behavior among the Brachyura exist; therefore the present study was undertaken both to satisfy this need in part, and to learn certain behavior patterns required for a comprehensive understanding of this crab. Inasmuch as data will be presented in detail at a later date, it will suffice to give here only a brief résumé of these findings.

It was not anticipated that territorialism, if present in this species, would be as well defined as that found among many vertebrates. The proportionately enormous crab population, the relatively small habitable area, and the tremendous biotic pressure upon littoral species tend to complicate interspecific associations and to make these associations obscure and comparatively difficult to study.

It was apparent from a 3-year period of extensive observations on this species that true territorialism with respect to life-sustaining activities as exhibited by many vertebrates does not exist. However, the refuges are characteristically defended with brisk determination; each crab selects the crevice best suited to it and thenceforth defends it from all intruders. The success achieved in the defense of an area is dependent upon the size and pugnacity of the individual. Two of similar size will fight viciously for a desirable crevice until the most virile of the pair succeeds, a behavior pattern reminiscent of the "peck order" first described for birds by Allee (1938). Large crabs apparently defend a small area immediately adjacent

to their refuges, whereas small individuals seem content to defend only the crevice itself.

On several occasions a crab was found in the same refuge for 2 successive days, indicating that some degree of stability is attained. The smaller crabs tend to remain in restricted areas and show more evidences of territoriality than do the larger crabs. However, the underlying factor here may not be innate territorialism but rather self-preservation, inasmuch as the crevices accepted by young crabs are sufficiently small to exclude the larger individuals which wander about the pool. The data secured seem to show that the virility order together with the number of desirable refuges in a tide pool combine to regulate the distribution of the animals.

The gregariousness of grapsoid crabs lower on the strand (*H. nudus* and *H. oregonensis*) in contrast to the individualism of *P. crassipes*, together with the independent existence of fossorial land crabs, may indicate that territorialism is progressively more highly developed as crabs become adapted to a terrestrial existence. It is likely that this trend toward territoriality is associated with the comparatively spacious *Lebensraum* extending landward from the strand, in contrast to the narrow stratified zones so characteristic of the littoral area.

Although these crabs live together in large numbers they neither exhibit co-operation with one another, nor manifest any tendency toward such communal existence as that displayed by many terrestrial arthropods. The writer has found no evidence that these animals associate for mutual aid either in foraging for food or for defensive purposes. Crabs appear to have their own refuges and are responsible for their own interests. In this respect they agree with other crustaceans, for although they possess an endless variety of structural adaptation suited to a multitude of habitats and modes of life, very few have taken advantage of the opportunities offered by a communal association among members of the same species.

DEFENSIVE MUTILATION AND REGENERATION

Defensive Mutilation

The ease with which *P. crassipes* severs its pereiopods, together with the high frequency of collected specimens found with regenerating appendages, makes it imperative that an investigation of these phenomena be made to evaluate their relationship to the general welfare of the animals. It is generally accepted by investigators of defensive mutilation that the automatic severance of an appendage from the body is a reflex act. However, not until recently (Wood and Wood, 1932) was the mechanism whereby this is accomplished fully determined, although it had been frequently discussed for more than a century. To comprehend the interpretations presented in the literature and the observations made on *P. crassipes*, it is necessary to clarify the definitions of the terms which have been applied to self-mutilation and closely allied phenomena. Since the term *autotomie* was introduced by Fredericq (1883), investigators have included under it the following closely associated but distinct phenomena:

Autopasy results when an outside agent is responsible for the severance of an appendage at a pre-formed breakage plane (Pieron, 1907).

Autotilly is the separation of an appendage at a pre-formed breakage plane with the assistance of mouth parts, chelae, or other pereiopods of the animal itself (Wood and Wood, 1932).

Autotomy refers to the reflex severance of an appendage without aid from any source other than from the appendage severed (Fredericq, 1883).

Autophagy is the act of consuming a part of the body, usually after severance from the remainder of the animal (Wood and Wood, *op. cit.*).

The failure of early investigators in this field to distinguish between the foregoing types of self-mutilation has resulted in the publica-

tion of descriptions of at least five distinct "self-mutilation mechanisms," each different and only two being partly correct (MacCulloch, 1825; Fredericq, 1882, 1883; Demoor, 1891; Wirén, 1896; and Paul, 1915*b*). Space does not permit a review of the historically significant mechanisms of self-mutilation; the reader is referred to Wood and Wood (*op. cit.*) for a synoptic résumé.

A knowledge of the morphological features of the appendages which are directly involved with self-amputation is a prerequisite for understanding the mechanism for severance in *P. crassipes*. Figure 15 serves to illustrate these features which, with their descriptions, will clarify the mechanism in this species.

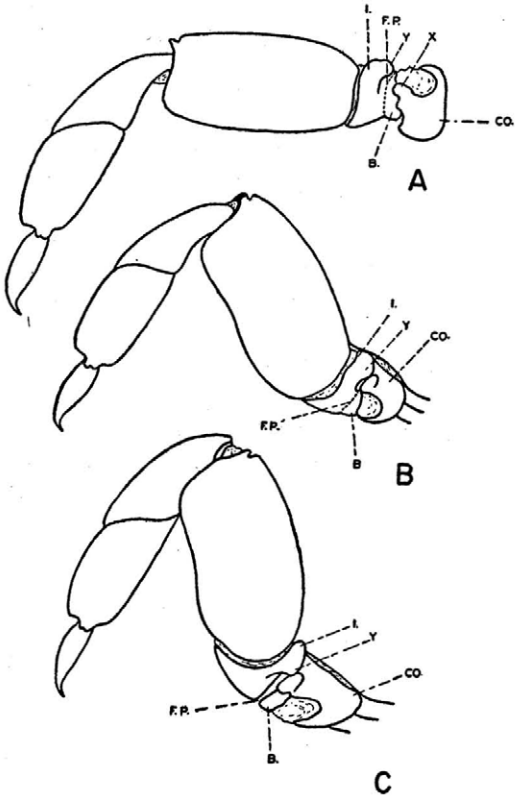


FIG. 15. Autotomy in *P. crassipes*; A, the pereiopod in normal position; B, the limb has been elevated until processes X and Y become contiguous; C, further levation has resulted in severing the appendage at the fracture plane. B., basis; CO., coxa; F.P., fracture plane; I., ischium; X, protuberance on coxa; Y, protuberance on ischium.

The *coxa* (Fig. 15, CO.) is a short, stout cylinder articulating with the sternum and epimeron and moving in an anteroposterior direction. A process which extends distally on the posterior side (X) is important in autotomy.

The *basis* (Fig. 15, B.) is an extremely short cylinder with a smaller diameter than the coxa. It articulates with the coxa and moves in a dorsoventral direction; the wide arthrodial membrane which connects the coxa and basis permits extensive movement. The basis, being narrow, slips in under the dorsal, distal edge of the coxa during extreme elevation, a condition essential for autotomy. The distal end of the basis is marked by a groove which encircles the appendage and separates the basis from the ischium, the two podomeres being fused.

Inserting on the anterodorsal edge of the proximal rim of the basis is the long slender tendon from which the fibers of the *anterior levator basis* (autotomizer muscle) arise. The muscle has widely distributed origins: from the anterior surface of the endopleurite, from the endosternite, and a few fibers from the epimeron and the dorsal surface of the coxa (Fig. 16, A.L.B.).

The *ischium* (Fig. 15, I.) is larger and wider than the basis with which it is immovably fused. On its dorsoposterior surface a protuberance (Y), which is important in the mechanism of autotomy, extends medially toward the body. None of the more distal segments are necessary for autotomy because it will occur in a normal fashion when they are removed.

The mechanism of autotomy set forth by Wood and Wood (1932) has been corroborated in all respects by this study on *P. crassipes*. Their observations on dead animals have been repeated on this species and were found identical. The rapidity with which the limb is autotomized makes it impossible to observe the process; therefore it is imperative that the observations be performed on a preserved specimen or on a complete appendage detached from the body with the autotomizer muscle intact.

To disclose the autotomizer muscle, windows were cut in the dorsal side of the coxa and

epimeron, and the wide arthrodial membrane between the coxa and ischium was removed (Fig. 16). By inserting forceps through the epimeral window the muscles inserting thereon could be grasped, and by tugging on each muscle it was possible to determine which was responsible for elevating the ischium—the *anterior levator basis.* The *posterior levator basis,* which inserts on the posterodorsal edge of the basis,

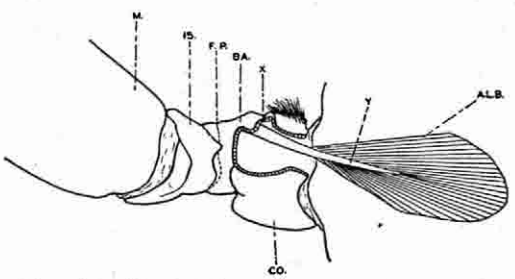


FIG. 16. The basal podomeres and autotomizer muscle of the left fifth pereiopod of *P. crassipes.* The integument on the dorsal side of the coxa and the arthrodial membrane between the coxa and basis have been removed to show the insertion of the *anterior levator basis.* A.L.B., *anterior levator basis*; BA., basis; CO., coxa; F.P., fracture plane; IS., ischium; M., merus; X, cut edge of coxal integument; Y, tendon of *anterior levator basis.*

is short and arises from the proximal edge of the coxa, hence it is not easily grasped through the epimeral window. This leaves only the *anterior levator basis* available for such an operation. By grasping the tendon (the fibers themselves tear too easily) with the forceps and holding a finger on the upper side of the merus to serve as the resistance, it was possible to simulate autotilly by pulling on the tendon. The break occurred at the fracture plane and proceeded with a minimum of effort. When the appendage was pulled or twisted without also pulling on the autotomizer muscle, breaks occurred at the arthrodial membranes between the podomeres. The foregoing observations serve to emphasize two significant points concerning mutilation: (1) the weakest point in the leg is not the fracture plane, and (2) the autotomizer muscle must be stimulated to contract before self-amputation can occur. Fredericq's application of a resistance (some force other than the crab's own body; e.g., placing a finger on the dorsal edge of the merus) influenced him to believe that some external force was indispensable, and it is the type of amputation which he described as *autotomie.* It has been shown above that this type of amputation is more aptly designated *autotilly.* Later workers discovered that the appendages could be severed without any form of external resistance.

Amputated appendages were commonly found in the aquaria if the water was stagnant or contaminated with decaying food. Inasmuch as no external agents were available, the crab must have shed its appendage or appendages by autotilly or autotomy. *P. crassipes* does employ autotilly and it is, perhaps, the method most generally used. Autotilly can be readily demonstrated by injuring the distal podomeres (with the exception of the dactylus). The limb anterior to the mutilated one is moved posteriorly and over the injured member; the injured member is straightened and moved upward while the anterior limb provides the resistance. The leg breaks at the fracture plane and autotilly occurs. It is accomplished hastily, the entire procedure occupying less than 2 seconds in healthy individuals.

Figure 15 illustrates the method whereby the morphological features of the coxa and basi-ischium, together with the autotomizer muscle, are alone responsible for the mechanics of autotomy. Autotomy may also be demonstrated on dead or preserved animals, although it is difficult to perform. Among living animals this method is perhaps the least utilized and has never been observed in this species; however, considerable circumstantial evidence set forth below serves to denote its presence. The procedure follows: The autotomizer muscle contracts, forcing the appendage dorsally; the basis, of less diameter than the coxa, slips inside the latter structure, allowing protuberance Y on the ischium to contact protuberance X on the coxa. The meeting of these two structures provides the resistance required to sever the limb when the autotomizer muscle is further contracted. The fracture originates at the dorsal side and travels ventrally.

Autotomy is difficult to perform because of the maximal contraction which the autotomizer muscle must exert on the rim of the basis in order to elevate the limb sufficiently high, together with the additional tension required to autotomize the appendage. Proof of the occurrence of this method was secured when two captive crabs severed all of the legs with the exception of the chelae and the fifth pair. Pereiopods 2, 3, and 4 probably were autotillized, but the fifth pair is articulated in a manner which prohibits the chelae from contacting it. Three days after the last autotilly, the fifth pair of appendages of one crab was severed. Five days after the last autotilly in the second crab, one of the fifth pair was severed. The foregoing behavior suggests two significant points; namely, (1) that autotomy of the type illustrated in Figure 15 must have occurred, and (2) that the long interval between autotilly and autotomy may possibly be attributed to the poor condition of the animals after the wholesale severance of most of their appendages. It is possible that the interval between autotilly and autotomy was a period of convalescence, during which the animals regained the vigor necessary to accomplish this type of mutilation. Several of the captive crabs severed pereiopods 2, 3, and 4 from one side; but few severed the fifth pair if those anterior had been cast previously.

In the laboratory a unique behaviorism designed to contribute to autotomy was observed during ecdysis. A crab which was having considerable difficulty in withdrawing the ambulatory appendages was observed to sever three limbs (right pereiopods 2, 3, and 4) by autotilly. The second pereiopod of the left side was likewise autotillized, but in an attempt to sever left pereiopods 3 and 4 (left pereiopod 5 was successfully exsheathed) the animal elevated the right side of the body until it described an angle of approximately 75° with the substrate. All podomeres of the left pereiopods rested on the bottom of the aquarium. In this manner the crab, in its weakened condition, brought the processes X and Y (Fig. 15) together and effected autotomy.

Autopasy is especially prevalent in this species because of its scurrying behavior. Crabs will sever a grasped appendage in a fraction of a second. To test the number of successive autopasies which an individual crab will voluntarily undergo when held by the tip of an ambulatory leg, 20 individuals were collected at random. Each animal was placed on the substrate in its normal habitat and a dactyl was held. The first ambulatory leg grasped was severed almost immediately by each of the individuals. An assistant rapidly re-collected the crabs. At no time did the crabs offer to employ the chelae in defense. In the second test another leg was held which was likewise severed; however, more time elapsed before autopasy ensued; each animal required from 2 to 10 seconds to complete the process. The re-collected crabs were put to a third test. At this time 11 of the 20 specimens attempted to defend themselves by employing the chelae; when this defense was frustrated, 16 of the 20 cast the third appendage. The time varied between 30 seconds and 2 minutes. After re-securing the animals a fourth leg was held. Without exception, each crab made violent slashes with the chelae. Three crabs severed the fourth leg in 45 seconds, 2½ minutes, and 3 minutes and 10 seconds, respectively. None of the remaining 17 animals would cast the fourth leg. All of them became placid and reluctant to move.

The reluctance of the animal to sever its chelae was evident. Without exception, when a cheliped was grasped, the free chela was immediately used to defend the animal. Whether this behavior was associated with the ability of the animals to move the chelae in the lateral and forward area or to some instinctive behavior to protect these valuable appendages is not known. When the free cheliped was successfully parried, autopasy occurred without exception. The second cheliped was cast but once in 20 tests.

Some investigators contend that autotomy cannot occur while the crab is in a soft-shelled condition; however, in *P. crassipes* autotomy,

autotilly, and autopasy all occur in crabs in the A_1 stage. It was soon discovered that the limbs of newly molted individuals could not be grasped or held in any manner because autopasy is effected rapidly at this time. Despite utmost care, autopasy has occurred on several occasions while newly molted animals were being measured. Moreover, appendages are frequently found in aquaria containing recently molted crabs, which indicates that autotilly is common prior to complete sclerotization.

Although cannibalism is prevalent when newly molted crabs are located in an aquarium with hard-shelled individuals, none of the latter has been observed to consume portions of a severed appendage, nor have any severed appendages been found from which portions had been eaten. It seems conclusive, therefore, that autophagy is lacking in this species. However, crushed appendages tossed into a tide pool are readily consumed. The lack of autophagy may perhaps be partially explained by the fact that the sclerotized integument precludes consumption of the potential food; however, it is strange that the soft appendages of a recently molted crab are not utilized.

Regeneration

Although sufficient time to pursue an exhaustive investigation into the subject of regeneration in *P. crassipes* was lacking, a cursory survey of this important activity of these crabs was made. The present study embraces the phenomenon of regeneration through three rather distinct avenues of approach: (1) Meticulous periodic examinations of several regenerating appendages were undertaken to disclose the events which occur during this process; (2) data were secured on regeneration and intermolt stages of a select group of crabs, not to provide a statistically accurate account of the regeneration by intermolt stages, but to find a few salient facts concerning regeneration, which, when correlated with the information now available on the intermolt cycle, might provide a framework for further investigation of this oft-occurring phenomenon in this species; and (3) to establish the frequency with which this species undertakes regeneration in its normal environment, the data for regenerating appendages on hundreds of collected specimens were analyzed.

Historically it is found that regeneration in decapod crustaceans has drawn the attention of biologists for more than two centuries. Réaumur (1712) first described the regeneration of legs of crabs, lobsters, and crayfish. Later, information on morphological development (Brooks, 1882; Herrick, 1896; Perkins, 1927; Yü, 1932; and a host of others) was combined with considerable experimental data chiefly presented by Zeleny (1905) and Emmel (1907) to formulate our present extensive knowledge of this phenomenon.

Before presenting the regeneration data for *P. crassipes*, a brief synopsis of the internal morphological transformations which occur from the instant of pereiopodal mutilation to the onset of regeneration of the new limb will be helpful toward an understanding of the external limb transformations which occur in this species. Our present histological and cytological knowledge of regeneration in decapod Crustacea stems primarily from macruran and anomuran types (Reed, 1904; Emmel, 1910; Paul, 1915*a*), with the latter worker contributing, in addition, some information on the brachyuran group. In general, all three groups follow the same fundamental pattern and differ only in detail. The following account is fundamentally based on regeneration in the hermit crab as described by Paul (*op. cit.*).

At the fracture plane the sclerotized strata of the integument are discontinuous for a part of the circumference of the leg. The columnar epithelial cells are greatly enlarged at this point and possess processes which extend inward, meeting those of the opposite side. These fibers mat together to form the diaphragm. The appendicular artery passes through a foramen, which it completely fills; but the foramen for the nerve is a funnel-like prolongation of the diaphragm which fits loosely about the nerve, thereby affording the venous blood a return

passageway. Paul has demonstrated that upon severance of the appendage both the artery and nerve retract from the diaphragm, and blood extravasates from the ruptured distal end of the artery. The increased pressure in the haemocoelic space forces together the funnel-like flaps which completely occlude the foramina. Therefore this mechanism supplants, in part at least, the earlier hypothesis (Reed, 1904) that a blood clot formed over the foramina, thus stopping the flow of blood. Actually some blood does pass to the outside of the diaphragm at autotomy because a layer of clotted blood covers the developing papilla for several days in *P. crassipes*, and has likewise been reported in other species.

The subsequent papilla formation is accomplished by the proliferation of cells from the free edges of the columnar epithelium. Emmel (1910) and Paul (1915*a*) have shown that blastematic cells which participate in regeneration of both the artery and nerve emanate from the epidermal layer, while the free ends of the severed artery and nerve contribute but little in the ensuing regeneration. The initial structure replaced is the diaphragm, a safety feature in the welfare of the crab; furthermore, differentiation within the papilla occurs from the fracture plane distally, never vice versa. Within a few days after autotomy, the epithelial cells form a layer over the stump and begin to proliferate at the center, initiating formation of the papilla, which is conspicuous a few days following autotomy. A significant feature described by both the above authors and substantiated by the present investigation is the lack of sclerotization of the regenerating appendage. This phenomenon is undoubtedly associated with the vast size increment from its papillary form to its functional manifestation after ecdysis. Throughout the entire papillary development the appendage is encased in a pliable sheath which is cast off during exuviation.

The initial information secured concerning regeneration in *P. crassipes* was derived from a study of 25 regenerating appendages on eight male and two female captive animals, each with one to five severed pereiopods. These animals, which were selected at random, ranged from 20.8 to 30.4 millimeters in width. Their intermolt stage frequencies were: C_1, one; early C_4, three; late C_4, three; D_2, two; and D_3, one. Several pereiopods were severed at ecdysis and thus provided an opportunity for study of regenerative progress from stage A_1. Daily observations included a check on the intermolt stage combined with a measurement and description of developing papillae. When observations were concluded 60 days later, five of the crabs were still living, three had succumbed during ecdysis, and two had died of other causes. Two crabs had molted and successfully regenerated their appendages, and several others were in advanced intermolt stages. Although the study was interrupted before adequate data concerning the relationships between regeneration and the intermolt cycle were secured, sufficient information was collected to clarify, in part, some of the nebulous data accumulated by pioneer investigators who were unaware of the uncompromising association between endysis and regenerational development. A description of the morphological features of regeneration in *P. crassipes* will be set forth first, followed by a synoptic account of its association with integumental development.

Three days subsequent to autotomy the blood clot appeared completely black. The time interval varied, however, from 2 to 4 days, and coincided with the latter part of stage A_2 or the early part of stage B_1. This clot was pushed outward from below by the proliferating epithelial cells until it was fractured on about the eighth day (but again the period varied from 6 to 10 days). The papilla was conspicuous 2 or 3 days later. The intermolt stage in which the papilla fractured the clot varied from B_1 to C_1. The interval between autopasy and the growth of the papilla to a length of 1 millimeter required about 11 to 16 days, although one individual developed to this degree in but 9 days.

The earliest indication of podomeric differentation was manifest when the papilla reached approximately 1 millimeter in length. Three depressions appeared at this time: two longitudinal, one on each side; and one horizontal, immediately below the apex. The longitudinal furrow marks the separation of the merus on one side and the carpus and propodus on the other; the horizontal depression denotes the articular area which separates the carpus from the propodus. The dactylus became visible a few days later, appearing as another longitudinal furrow at the base of the papilla on the side containing the propodus. These depressions deepened, and another near the base of the merus indicated the division between this podomere and the basi-ischium. Regeneration in the chelipeds was slightly different from that in the ambulatory appendages. The papilla of the former was larger and capitate. Only two longitudinal furrows were conspicuous laterally, and the furrow which marks the separation of the dactyl from the propodus differed from that found in the ambulatory legs. The dactyl of the cheliped is in apposition to the extended finger of the propodus, therefore the furrow is single, longitudinal, and perpendicular to the furrows which indicate the junction of the merus and propodus. The remaining podomeres developed similarly to those of an ambulatory appendage.

External differentiation of the podomeres was complete in approximately 18 to 21 days from time of severance, by which time the animal reached the C_2 stage. Crab No. 10 attained this stage in 13 days. The precocious development of the papilla of crab No. 10 is significent because autotomy occurred in early C_4, and complete regeneration ensued prior to the first post-autotomal molt. Of the five C_4 crabs from which limbs were removed, only crab No. 10 accomplished complete regeneration by the first molt.

Pigmentary deposition in the podomeres took place in the sequence of podomeric differentiation; it began on the merus and propodus, later progressed to the carpus and dactylus, and reached the basi-ischium last. Pigment was apparent about 24 to 27 days after severance of the appendage; crab No. 10 exhibited pigmentation as early as the sixteenth day. At the onset of pigmentation the papillae varied from 1.5 to 2.0 millimeters in length.

Appendages severed during stage A_1 required between 30 and 33 days to develop papillae 4 millimeters in length; crab No. 10 reached this stage in 18 days. At this time, the crabs which underwent ecdysis before papillary development had reached stage C_3 or early C_4.

Upon the attainment of stage D_4 the papillae which exhibited complete podomeric differentiation reached a length of about 7 millimeters. Of four completely developed pereiopodal papillae, three measured 7.1 millimeters and one measured 7.2 millimeters immediately prior to ecdysis. During the investigation two crabs had papillae which grew in an anomalous manner. Both these papillae were severed at ecdysis and new, normal papillae were later observed. It is evident, therefore, that normal regenerative processes may be modified. However, the absence of malformed appendages in wild crabs, combined with the exuvial autotomy of anomalous papillae, suggests that aberrantly formed limbs rarely, if ever, succeed in reaching a functional condition.

The present study on captive animals, in addition to extensive collection of wild crabs with regenerating limbs, has shown that two or more severed limbs will attain the same degree of regeneration before ecdysis regardless of when autotomy occurred before stage C_4. However, the data at hand are insufficient to ascertain whether or not regeneration is accelerated when mutilation occurs in an intermolt stage prior to C_4. One would surmise that acceleration was inevitable, and the information available strongly suggests this phenomenon.

To obtain information concerning regenerational development and the intermolt cycle of wild crabs, 203 crabs were collected and examined during March, 1941. Of this number, 58 had nearly mature papillae (i.e., papillae with

a length in excess of 4 millimeters were considered nearly mature). A comparison of mature papillae and intermolt stages is indicated in Table 5. It is shown that papillae may closely approach maturity by the termination of stage C_3, which fact, when combined with laboratory data, indicates that severance probably occurred at ecdysis or shortly thereafter. However, most do not attain maturity until stage C_4 is reached. The laboratory data likewise confirm this observation. The diminished representation of mature papillae in period D is directly proportional to decreased frequency with which animals in period D are found in nature.

TABLE 5

COMPARISON BETWEEN THE INTERMOLT STAGE AND FREQUENCY OF NEARLY MATURE PAPILLAE IN WILD SPECIMENS OF *P. crassipes*.

INTERMOLT STAGE	NUMBER OF CRABS EXAMINED	NUMBER OF NEARLY MATURE PAPILLAE
C_3	33	3
C_4	96	32
D_1	40	13
D_2	27	8
D_3	7	2
Total	203	58

The foregoing observations on regenerative progress and integumental synthesis have disclosed some facts which not only effect a partial clarification of certain heretofore nebulous concepts of regeneration, but suggest new lines of approach toward the solution of pertinent problems. These data indicate that within intermolt stage C_4 there is a critical period before which regeneration of a complete appendage will occur prior to the molt, and after which complete regeneration will not occur prior to the molt. Only one appendage of six severed during the C_4 stage in the captive animals completed its regeneration before the molt, and this one was severed during a very early C_4 stage. None of the five appendages severed during period D advanced beyond the blood-clot stage; whereas all of the 19 appendages severed in early intermolt stages underwent complete development; and those crabs which successfully underwent ecdysis had completely regenerated limbs. Stage C_4, it will be recalled, marks the conclusion of the synthesis of the old integument, and all subsequent stages are concerned with its partial dissolution. It seems likely, therefore, that any regeneration which occurs prior to the complete synthesis of the old integument probably retards that synthesis until the regenerating member slackens its development in the latter stages. Meager substantiation of this hypothesis was secured from crab No. 10, which, at the onset of regeneration, was in an early C_4 stage. Complete regeneration ensued prior to ecdysis, requiring 29 days from C_4 to D_4—a longer period than that required by all other crabs in the experiment, although several were larger and would be expected to require even additional time if other conditions were equivalent. It seems reasonable to assume that experiments on regeneration may be performed with considerable accuracy if the investigator is cognizant of the transformations which occur during the intermolt cycle and is able to ascertain them without error. It is clear that the inability of former investigators to diagnose the intermolt period accurately has clouded the results of most of the experimental investigations on regeneration in decapod Crustacea.

Measurements were made to ascertain the growth of the regenerating limbs on captive crabs for at least three successive molts. The graphic analyses of pereiopodal growth (Fig. 17) indicate that three molts are undergone before regenerating limbs reach the size of the corresponding limb on the opposite side of the animal. After the first post-regenerative molt the limb extends to about three quarters of its normal size (Pl. 2, Fig. 1).

The probability of appendicular regeneration occurring from some point other than the fracture plane in *P. crassipes* was also investigated. Morgan (1902) demonstrated that this phenomenon could occur in hermit crabs, not only from points distal to the fracture plane but also from regions proximal to it. Although no controlled experimentation on *P. crassipes*

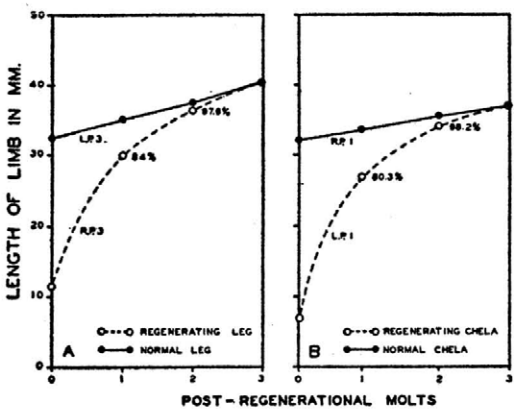


FIG. 17. Comparative growth of normal and regenerating appendage of *P. crassipes* at ecdysis. A, growth of the third pair of pereiopods; B, growth of the chelae. The percentages indicate the size of the regenerating limb compared with the opposite normal limb at a certain intermolt interval. L.P., left pereiopod; R.P., right pereiopod.

was undertaken, sufficient observations on both captive and wild crabs have been made to describe this feature in some detail. With the exception of the dactyls, regeneration from any point in the appendage other than the fracture plane has never been recorded in an examination of well over 3,000 crabs in collections and of countless numbers observed in the field. It seems probable, therefore, that under normal conditions this species always severs the limbs at the fracture plane. The regeneration of portions of the dactyls is common in nature, and, because of their utility in diagnosing intermolt stages (p. 152), several crabs which had regenerating dactyls were available for laboratory observation over extensive periods. The papilla of the dactyl grows approximately to its normal size; but, since the regenerating portion of the dactyl is invested by an external membrane similar to that covering the papilla at the fracture plane, the papilla displays no spines. The investing membrane is cast at ecdysis and the new dactyl emerges in its normal form. In wild crabs the frequency of regenerating dactyls is highest for the chelae, doubtless the result of the vigorous activity involving the chelae which often leads to the fracture of the distal portion of this podomere. One such example is shown in Plate 2, Figure 2. It is significant and distinctly advantageous to the crab that an injury to the dactyl does not result in autotilly or autotomy. It was found that injury to all podomeres except the dactyl stimulated virtually immediate amputation at the fracture plane. It has long been known that the thoracic nerve must be stimulated to effect both autotilly and autotomy; and since branches of this nerve do not extend into the dactylus (Pearson, 1908), injury to this distal podomere is insufficient to activate the mechanism of amputation.

Of the several thousand crabs handled during this study, approximately 30 per cent had one or more regenerating appendages. Such a high frequency of severed appendages implies a relatively precarious existence which is reflected in the ease of amputation and relatively frequent molts. If, for example, comparisons are made between *P. crassipes* and those brachyuran species residing lower on the strand—or below low-tide level—with respect to type of habitat, activity, predation, and capability of self-amputation, marked differences are manifest immediately. Hundreds of crabs (*Cancer magister* Dana) brought into wholesale markets by fishermen have been examined for regenerating appendages. Relatively few regenerating appendages were found; indeed, to find one was rather rare. Autopasy is less easily accomplished in this cancroid species and much more time is required for this activity than for the process involved in *P. crassipes*. Thus the infrequent regeneration in *C. magister* is probably associated with the difficulty of self-amputation, which in itself may be an adaptation to the infrequent molts and the comparatively more placid existence of this crab. Other cancroid crabs (*C. productus* Randall and *C. antennarius* Stimpson) which occur in the intertidal zone were examined similarly and found to exhibit characteristics comparable to *C. magister*.

Differences between *P. crassipes* and the more sluggish and less-exposed cancroid crabs significantly portray many aspects of the evolutionary

changes within the Brachyura, which are, perhaps, the result of intense biotic pressure along the littoral area. It is certain that the cancroid crabs mentioned above could not subsist high in the littoral zone. *P. crassipes,* on the other hand, has become adapted to its exposed littoral horizon by achieving, among other things, the ability of facile self-amputation and rapid regeneration. These features have undoubtedly contributed to its success in reaching and establishing itself in an area rich in food materials, notwithstanding the fact that it is exposed to countless dangers.

PREDACEOUS AND PARASITIC ENEMIES OF *P. crassipes*

The countless dangers encountered by *P. crassipes* include relatively few predators but each kind occurs in rather high frequency. Among the vertebrate predators, the gulls (p. 170) are perhaps the most important. The flight reflex exhibited by *P. crassipes* when a gull or its shadow passes by provides some circumstantial evidence pointing to the significance of these birds, although their successful predation on the crabs has never been noted. Frequently gulls have been observed dipping suddenly over the rocks where the crabs reside. The absence of protective coloration in this species would seem to make them effective targets for this winged predator. The numerous crab skeletons found on wharves below gull perches substantiate the predatory nature of the gulls with respect to the shore crabs. Rats which frequent the littoral area during the night probably prey upon these nocturnally active crabs, and the inability of the crabs to detect danger at night would seem to make them easy victims. This crab does not escape the extensive littoral predation of man. Although the crabs are disregarded as a food source, small boys and even adults have frequently been observed in attempts to extricate the crabs from their crevices. Though most of the attempts fail, the crabs are often severely mutilated. To escape capture, *P. crassipes* will back deep into a crevice and elevate the carapace until the rough striae on the protogastric lobes are pressed tightly against the rock. It is virtually impossible to extricate a crab in this position because the striae serve as an effective resistance against the rock, making the animal practically immovable within the limits of the strength of the body parts. The chelae are freed for defense in this position, and continued molestation will eventually result in the surrender of these appendages. Usually the exoskeleton is crushed before the animal can be withdrawn from its wedged position.

In general, it may be stated that *P. crassipes* is not easy prey for vertebrate predators—except at night—for a number of reasons: (1) Their alertness when exposed and their agility when disturbed often enable them to escape from predators; (2) they possess an exceptional ability to amputate the appendages that are grasped; (3) during diurnal hours they tend to remain in the vicinity of their refuges.

Among the invertebrate predators, the larger sea anemones (*Bunodactis elegantissima* and *Anthopleura xanthogrammica*) are known to consume small crabs. Portions of *P. crassipes* have been observed protruding from the stomodaea of these species. It is a common occurrence in the high-tide pools at Monterey to find bits of *P. crassipes* integument among a *Bunodactis* bed, and feeding experiments conclusively indicate that anemones will readily utilize the crabs for food. None of the carapaces of the devoured crabs taken from anemones measured, or would have measured, over 20 millimeters in breadth. Large crabs thrown on a *Bunodactis* bed invariably elude attempts at capture. Smaller crabs are much less successful.

It is necessary to consider the crabs themselves as potential enemies of each other. Cannibalism is frequent and is a perpetual threat to recently molted individuals.

The larger animal ectoparasites common to littoral crabs are exceedingly sparse on the *P. crassipes* found along the coast of central California. No macroscopic ectoparasites were ever found on collected specimens. A detailed

examination was made of 150 individuals collected at Monterey. These were packed in ice for 3 hours, and subsequently preserved in 10 per cent formalin. The branchiostegites and gills were removed; both, plus the epimeral wall, were washed with a stream of water; the water and contents were centrifuged, and the material was searched for parasites exclusive of protozoans. No parasitic species were encountered. Only one reference to parasitism on this species in California occurs (Baker, 1912), and this reference concerned an undescribed parasitic isopod located in the branchial cavity. Pearse (1931) indicates that Japanese specimens of *P. crassipes* have a high degree of infestation with the rhizocephalan, *Sacculina.* However, since *P. crassipes* does not occur abundantly within the more northerly range of *Sacculina* and *Peltogaster* along the western American coast, a low incidence of infection might occur in the area of overlapping ranges, but infected lined shore crabs have never been found.

REPRODUCTION

Sexual Dimorphism and External Genitalia

Only slight sexual dimorphism occurs in this species except for the abdomen, which is triangular in the male and subcircular in mature females. Sexual variation of the abdomen becomes macroscopically apparent in crabs as small as 6 millimeters in carapace breadth. In females a progressive abdominal transformation ensues from a triangular shape in young crabs to the attainment of the subcircular form at maturity.

Extensive sexual differences are noted when the abdomens are extended. The first and second abdominal appendages of the male are modified for use as the intromittent organ; the initial pair is the larger and has a tubular form, whereas the second pair is considerably smaller and is located directly posterior to the tubular pair. The second pair functions as plungers or pistons working inside the tubular appendages; together they accomplish the transfer of the spermatophores into the genital apertures of the female. To effect the transportation of spermatophores from the coxal aperture on the fifth pereiopod to the intromittent organ, a sheath which arises from the coxa encloses the terminus of the vas deferens and extends to the base of the first intromittent appendage. This sheath functions as a funnel to convey the genital products into the intromittent organ. The flexed abdomen covers the coxal opening and sheath.

When the abdomen of a female is extended, the oviducal apertures on the third thoracic sternite and four pairs of large abdominal pleopods are apparent (Pl. 2, Fig. 6). The copulatory structures of the male are inserted into the vulvae during impregnation. Inasmuch as the intromittent organs of the male are restricted to movement in an anteroposterior direction and the vulvae of the females are immovable (except perhaps for slight stretching in stage A_1 just after ecdysis), it is evident that a successful spermatophoric transfer could hardly be achieved between crabs differing greatly in size. The ova issue through the vulvae and become adherent to the endopoditic setae of each pleopod, thereby forming the egg mass (Pl. 2, Fig. 3).

Age and Size at Sexual Maturity

The age and size at sexual maturity were ascertained by a comparison between the size range of the total number of ovigerous females collected on the coast of central California, together with a microscopic examination of the ovaries of 50 selected females whose carapaces ranged in width from 10 to 24 millimeters. The size range of ovigerous females collected during the most important spawning period is presented in Table 6. The most diminutive ovigerous female examined among wild specimens measured 16.9 millimeters in breadth. The records secured from dissections of females selected for size during the height of the spawning season are set forth in Table 7. It is obvious, from the data provided in Tables 6 and 7, that sexual maturity in females is achieved when the carapace breadth measures approximately 15 millimeters at about the eleventh or twelfth month after hatching.

TABLE 6

SUMMARY OF THE SIZE FREQUENCIES OF OVIGEROUS *P. crassipes* COLLECTED DURING THE FOUR IMPORTANT SPAWNING MONTHS.

MONTH	NUMBER OF FEMALES COLLECTED	NUMBER OF OVIGEROUS FEMALES	RANGE OF WIDTH (MM.)	PERCENTAGE OF OVIGEROUS FEMALES
May	20	5	28.5–41.5	25
June	151	61	18.7–39.2	40
July	362	112	17.8–39.7	31
August	626	144	16.9–44.0	23

Fifty selected male crabs were examined to ascertain their size and age at sexual maturity. The abdomens of the male crabs were extended, after which the genital sheaths about the vas deferens were excised and transferred to glass slides and examined microscopically for the presence of spermatozoa. A summary of the information secured is presented in Table 8. A comparatively precocious sexual maturity is evident for males. Adulthood is attained in approximately 7 months, at which time the crabs measure about 12 millimeters in breadth. Despite this early maturity, the males do not participate in reproductive activities until the second year unless they were hatched within the first 3 months of the year.

Most adult females become ovigerous sometime between April and September (Table 6). However, concrete evidence exists to show that berried females infrequently occur during the remaining months. Ricketts and Calvin (1939) note that berried females may be taken in such divergent months as February and June. Moreover, the writer has collected the megalops stage of this crab at Monterey during March, which indicates that hatching occurred in the latter part of January and, inasmuch as incubation required at least a month, the female involved became ovigerous in the latter part of December. Off-season spawning is not uncommon among the decapod Crustacea. Herrick (1909) has noted it in the lobster, and Broekhuysen (1936, 1941) has found it to be characteristic of two other shore crabs, *C. maenas* and *C. punctatus.*

Copulation and Impregnation

Pre-nuptial pairing or exhibitionism is lacking in this species, although the former is prevalent among the larger Brachyura (Williamson, 1903; Hay, 1905; Churchill, 1918). Moreover, the actual onset of copulation has been noted but once during this study, although several captive and wild crabs have been found *in coitu* less than a minute after they had been observed

TABLE 7

RECORD OF THE AGE AND OVARIAN DEVELOPMENT OF 50 SELECTED FEMALES OF *P. crassipes* COLLECTED ON JUNE 11, 1941.

BREADTH (MM.)	NUMBER OF CRABS	AGE* (MONTHS)	EGGS†	OVARIAN DEVELOPMENT
20.0–24.0	4	14–16	+	eggs large; ovary gravid
18.0–19.9	4	13	+	eggs large; ovary gravid
17.0–17.9	6	12	+	eggs medium-sized; ovary well-developed
16.0–16.9	5	12	+	eggs medium-sized; ovary well-developed
15.0–15.9	7	11	+	5 ovaries developed; 2 undeveloped
14.0–14.9	7	10	—	ovary undeveloped
13.0–13.9	6	8–9	—	ovary undeveloped
12.0–12.9	5	7	—	ovary undeveloped
11.0–11.9	3	6	—	ovary undeveloped
10.0–10.9	3	5	—	ovary undeveloped

* Ages were determined from Figure 10, page 167.
† A plus sign (+) indicates that eggs were present; a minus sign (—), that they were absent.

as separated individuals. The actual copulatory position is, therefore, assumed with rapidity. The infrequent observations of copulation, when compared with the vast number of hours of observation both in the laboratory and field, would indicate that copulation occurred chiefly at night or that it persists for a very brief interval. The present data strongly favor the former supposition.

TABLE 8

SIZE AND AGE AT ADULTHOOD (DETERMINED BY PRESENCE OF SPERMATOZOA) OF 50 MALE *P. crassipes* TAKEN ON JUNE 13, 1941.

BREADTH (MM.)	NUMBER OF CRABS	AGE* (MONTHS)	SPERMATOZOA
22.0–26.0	6	15–16	many
20.0–21.9	8	14	many
16.0–19.9	7	11–14	many
14.0–15.9	8	10–11	few to many
12.0–13.9	8	7–10	none to few
10.0–11.9	7	5–6	none to few
8.0–9.9	6	4–5	none

* Ages were determined from Figure 10, page 167.

Several close-up observations of copulating pairs have disclosed a constant positional pattern. Contrary to all descriptions of the copulatory act in other Brachyura, in this species it is the male which lies on its carapace below the female. The second, third, and fourth pereiopods of the male are placed between those of the female, and the dactyls are hooked over the lateral edge of her carapace. The fifth pereiopods of the male are looped around the posterior side of the corresponding appendages of the female, and the dactyls are hooked at the posterolateral edges of her carapace. The ambulatory appendages of the male, therefore, serve to grasp the female. The chelae are generally flexed in their normal folded position; however, at intervals those of the male are employed to grasp the female, and occasionally are utilized for protection from the thrusts of the female's chelae directed toward the male's oral area. The abdomen of the female completely covers that of the male, that of the latter being below the abdomen of the female. In this position the ventral surfaces of each member are contiguous, and the action of the penes is difficult to observe.

Although difficult to follow from above or below, impregnation was observed upon two occasions from the side. The abdomen of the male moved slightly forward and back with the penes inserted only a short distance into the vulvae.

Although the infrequent observations of copulation in this animal suggest brevity, the data secured for *P. crassipes* indicate extreme variability and comparatively long duration. In one field observation, in which impregnation appeared successful, the pair were *in coitu* for 45 minutes. Upon another occasion captive crabs were observed in copulation for 6 minutes (the onset was unnoticed) prior to separation. After the separation the male partially flexed and extended its abdomen arhythmically and, whenever the male approached its mate, the abdomen oscillated with increased tempo. In addition, this male repeatedly elevated and depressed its right cheliped. It seemed apparent that impregnation had not been completed. A copulatory act by another captive pair occurred and lasted for 15 minutes. When the crabs separated, they stood with their flexed chelae contiguous and the abdomens of both moved briskly; however, copulation was not resumed. Copulation by a third pair lasted for 20 minutes. The animals frequently moved about the aquarium while the female supported the suspended male. Another pair were *in coitu* for 5 minutes prior to separation. Several hours later the pair was again observed in copulation which persisted 4 minutes. It is highly significant to note that all the females mentioned above, comparable to most accounts in the literature, were in stage A_1, while the males were in C_3 or above. On the other hand, Broekhuysen (1941) indicated that copulation in *C. punctatus* occurred only between hard-shelled crabs.

Some anomalous copulatory behavior observed both in captive and wild crabs aided in apprais-

ing the mating phenomenon. A hard-shelled male was placed in an aquarium with a newly molted female and her exuvia. Twenty minutes later the male grasped the exuvia with the chelipeds and turned over on its back in the normal copulatory position. Throughout the struggle to arrange the exuvia in the correct position, the abdomen of the male oscillated rapidly back and forth. This abortive struggle persisted for 5 minutes after which the male righted itself and moved away. Although the male was willing to copulate, a fact deduced from its behavior with the exuvia, no attempt was made to engage the recently molted female. The endopoditic setae of the exuvia above were examined and found to contain empty egg capsules (Pl. 2, Fig. 5), which indicated that the non-copulating female described above had been ovigerous during the preceding intermolt interval. On another occasion an attempt at copulation was observed between a pair of crabs under a ledge high above the adjacent tide pool. The animals separated 5 minutes after they were discovered. The female was collected and found to be ovigerous. The foregoing anomalous behavior patterns seem to indicate that the males exhibit but slight discrimination toward their mating partners.

Copulation in this species occurs at least once yearly and is suspected to take place twice annually in some crabs. Recently molted females whose exuviae bore empty egg capsules on the endopoditic setae invariably exhibited empty spermathecae; subsequent impregnation, therefore, would be required during the following breeding season, or later in the same breeding season, providing a second batch of eggs were extruded. In many other Brachyura possessing far more extended intermolt intervals, it has been found that one impregnation suffices for the fertilization of the eggs of several egg batches which are expelled within a single intermolt interval (Williamson, 1903; Churchill, 1918; Broekhuysen, 1936, 1941).

Extrusion and Incubation of Ova

Although the interval between impregnation and spawning in *P. crassipes* has not been ascertained, its direct association with the intermolt cycle enables one to estimate the interval with considerable accuracy. Inasmuch as eggs are never extruded prior to stage C_3, the interval between impregnation and extrusion of eggs will depend directly upon the size of the female and will vary from approximately 16 days for small-sized, mature females to 25 days for large females.

Fertilized ova are expelled from the body of the female through the vulvae located on the thoracic sternum. They become attached to the fine endopoditic setae of the four pairs of pleopods located on the second to fifth abdominal metameres. These pleopodal endopodites are clothed for the most part with long, fine setae which are simple throughout, with the exception of a few which branch at the base. With the exception of the proximal segment, these setae arise in distinct bundles from each endopoditic segment (Fig. 18). The tufts arise only on the medial, lateral, and posterior surfaces of the endopoditic segments; the anterior surface is naked.

The general appearance of the egg mass has suggested its usual designation, the "sponge." Eight tufts or clumps of eggs are present, which correspond to the eight abdominal endopodites. These tufts are so crowded with ova that they become contiguous and appear as one mass. The sponge of a female measuring 32.0 millimeters in breadth is a rounded mass approximately 12 millimeters long by 40 millimeters wide by 12 millimeters deep (Pl. 2, Fig. 3). The eggs appear black to the unaided eye, but when viewed microscopically with transmitted light they are deep brown. The abdomen is forced back by the sponge until it describes a 60° angle with the sternal surface of the thorax and is curved behind the egg mass. A basket-like cavity which shields the egg mass is formed by plumose setae of the pleopodal exopodites (Fig. 18) and by the lateral margin of the abdominal tergites.

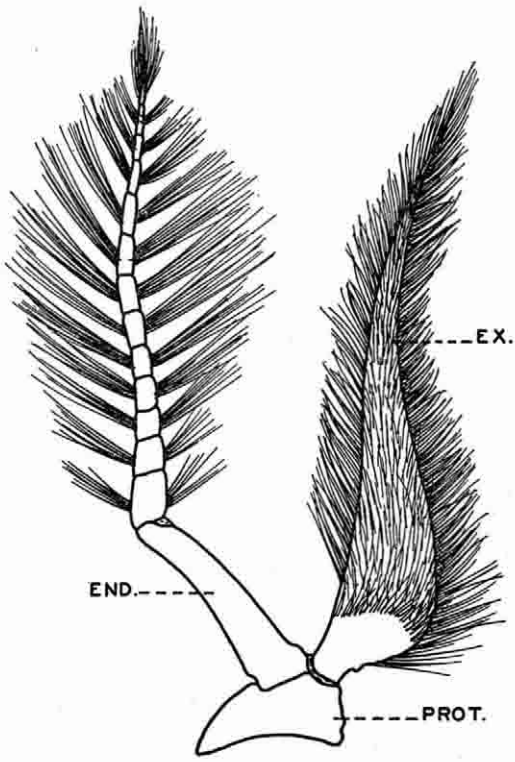


FIG. 18. Front view of the second abdominal pleopod of *P. crassipes* from right side. END., endopodite; EX., exopodite; PROT., protopodite.

The number of eggs extruded at one time seems to vary directly with the size of the crab. To estimate the number of ova contained in a sponge, an ovigerous female 36.5 millimeters in carapace breadth was selected. Each of the eight endopodites which bore the sponge was removed and compared. All contained approximately the same number of eggs; consequently the eggs adherent to one endopodite were counted and the sum multiplied by eight, which yielded a product of 48,604. Although this figure is an estimate, it can be reasonably assumed that the sponge of an average-sized female will contain approximately 50,000 ova. This number is considerably less than that estimated for *Callinectes* (Smith, 1885; Paulmier, 1901; Churchill, 1918) and slightly less than Williamson's (1903) estimate for *C. pagurus*. No information concerning this subject for crabs of a size comparable to *P. crassipes* is recorded. Inasmuch as the size of ova differs but slightly in all the crabs noted above, it seems probable that the enormous number of eggs which comprise the egg mass of the larger Brachyura is correlative with the size of the animals.

Excellent opportunities for critical study on the incubation of the ova were presented by captive females which expelled their ova in aquaria. Observations were made at 3-day intervals throughout the entire incubation period. A few eggs were removed from the setae, examined grossly, and measured. Inasmuch as these data were approximately uniform for four females under observation, they were averaged and are presented in summary in Table 9.

The foregoing data show that the incubation period was approximately 29 days. Other ovigerous females under observation carried eggs from 26 to 31 days. The significance of this incubation interval to the intermolt cycle has been discussed on page 153. Although a uniformity in size of eggs was apparent throughout development, it was found that when first expelled, the ova were misshapen and abnormally lengthened. Immediately after expulsion, the eggs actually shortened. It was further evident that during incubation the ova lengthened proportionately more than they broadened. This differential growth is undoubtedly a manifestation of the extensive elongation of the larval crab in an anteroposterior direction.

All of the captive ovigerous females exhibited irregular abdominal movements. These movements, which were accomplished by moving the abdomen backward and forward in jerky arhythmic beats, probably served to aid in maintaining efficient aeration of all the eggs in the mass. The wafting motion separates the eggs and thus permits the water to circulate among them. It is virtually impossible for water to circulate in the densely packed, stationary sponge. Ovigerous females in tide pools likewise wafted the abdomen, signifying that the movement is not merely an adjustment to tepid and less-aerated, laboratory sea water. The rate and periodicity of this wafting procedure were

TABLE 9

SUMMARY OF THE INCUBATION TIME, SIZE, AND GROSS DEVELOPMENT OF THE OVA OF CAPTIVE *P. crassipes* DURING JUNE, 1940. (MEAN AQUARIUM WATER TEMPERATURE, 16.2° C.)

WIDTH (MM.)	LENGTH (MM.)	DAYS AFTER EXPULSION	GROSS DESCRIPTION OF DEVELOPMENT
285	320	0	uniformly dark brown; many zygotes, others in 4–8-cell stage, all blastomeres large; no perivitelline membrane apparent
286	311	3	uniformly dark brown; blastomeres filling capsule; homogeneous; no perivitelline membrane apparent
288	310	5	uniformly dark brown; blastomeres smaller and more numerous; slight withdrawal of blastomeres from one section of the capsule reveals perivitelline space
291	314	8	uniformly dark brown; blastomeres very numerous; further asymmetry in blastomeric bulk reveals greater perivitelline space
294	316	10	uniformly dark brown; differentiation progressing; no pigment deposits present; blastomeres occupy about 0.6 of egg capsule
298	328	13	differentiation advanced; no pigment deposits; yolk cells in one part of cell mass only
312	351	18	highly differentiated; heart not beating
320	358	20	highly differentiated; heart beating; structures plainly visible; few ova on bottom of aquarium
324	368	24	no ova hatched; heart beat stronger, irregular (approximately 82 beats per minute)
		29	all ova on bottom of aquarium; many hatched

highly variable and apparently had no relationship to the degree of embryological development.

Both captive and wild ovigerous females were noted to thrust the chelae into the egg mass frequently, and to move the ova about in a manner which resembled a preening behavior. When the chelae were inserted into the sponge, the abdomen oscillated violently. Frequently, material which appeared to be ova was conveyed to the mouth. The writer believes that this preening or cleansing behavior is not associated with actual ingestion of the eggs, inasmuch as they thickly covered the bottom of the aquaria subsequent to this activity. It is possible that accidental plucking of the eggs resulted from attempts to remove foreign particles from the egg mass. Most of the ova observed on the bottoms of the aquaria after this cleansing activity had a short portion of the funicle attached, indicating that they had been severed from the setae. Frequently, broken setae with several attached ova were found. The severed eggs were invariably viable regardless of the developmental level.

The behavior of wild, ovigerous females with respect to submersion proved somewhat unusual and contrary to expectation. They frequently wandered up a rock surface and remained motionless in the direct sun for lengthy periods—1 hour and 15 minutes on one occasion, and 5 minutes less than that on another. Both these females were observed on the same day during which the air temperature was 72° F. It was further noted that in collections, the proportion of females increased during the breeding season, a fact which indicates that the ovigerous condition does not necessitate a sequestered existence. It seems likely, therefore, that the embryos demand no more than a minimum of submersion; further, the proportionately greater number of berried females found on the rocks than in tide pools may be associated with some biological requirement such as increased warmth to permit the maximum tempo of embryonic development.

The expulsion of more than one batch of eggs a year has been recorded for several of the Brachyura (Churchill, 1918; Broekhuysen, 1936, 1941). Although no direct evidence of a

second sponge within a single breeding season is available for *P. crassipes,* certain circumstantial evidence is sufficiently significant to remove the occurrence from doubtful rank. First, examinations were made of the ovarian development of berried crabs; and second, an examination of the ovarian development of recently molted female crabs, which might have been berried during the previous intermolt interval, was undertaken. Information on previous egg-bearing of recently molted females was secured through an examination of the endopoditic setae of the exuviae. The data concerning the ovarian development of ovigerous females are summarized in Table 10.

The gravid ovaries of many berried females during the height of the breeding season contribute significant evidence to the support of the writer's supposition that a second batch of eggs would be extruded within the 3 to 4 months remaining in the breeding season. However, it is to be noted that a few of the ovigerous females which, at the time of collection, had carried the expelled eggs about halfway through the incubation period exhibit very undeveloped ovaries. It is probable that these females would not extrude a second sponge in the time which remained in the spawning season.

Nine females in stage A_2 and their exuviae were collected in June, 1941, for an examination of their present ovarian development and of the endopoditic setae of the exuvia of each, to ascertain whether or not they had been ovigerous during the preceding intermolt interval. Only one had been ovigerous in the preceding intermolt interval and the ovary in this newly molted crab was ripe and gravid. Six of the others had small, undeveloped ovaries; two had ovaries which were nearly ripe, with ova of medium size. The outstanding feature of the data presented in Table 10, when associated with the data set forth immediately above, is the disclosure that an entire intermolt period may intervene between periods of sponge production. Inasmuch as the periods of ecdysis in this species are relatively frequent, it is not unreasonable that such a phenomenon should occur within the extensive breeding season. Exceptions to this behavior occur; e.g., it seems certain that the animal which contained the gravid ovary and which had a record of egg-bearing during the preceding intermolt interval would have become ovigerous for the second time in consecutive intermolt intervals. Whether or not the remaining crabs had been ovigerous earlier in the spawning season is conjectural. Some of the larger specimens probably had been; whereas the smaller individuals which contained, for the most part, relatively undeveloped ovaries probably would not have become gravid until the latter part of the spawning season. It seems probable, therefore, that the periodicity of gonadal development varies, not only between individuals, but within a single individual in

TABLE 10

THE SIZE, INTERMOLT STAGE, AND OVARIAN DEVELOPMENT OF OVIGEROUS FEMALES OF *P. crassipes* COLLECTED DURING JUNE, 1941.

CARAPACE BREADTH (MM.)	INTERMOLT STAGE	CONDITION OF INCUBATING EGGS	OVARIAN DEVELOPMENT
27.0	C_3	eyes visible	ripe, gravid
32.4	C_3	yolky blastomeres	ripe, gravid
31.9	C_4	blastomeres to one side	young, undeveloped
26.7	C_4	highly differentiated	ripe, gravid
30.3	C_4	highly differentiated	nearly ripe, gravid
26.5	C_4	eyes visible	ripe, gravid
36.0	C_4	yolky blastomeres	very young, undeveloped
26.4	C_4	highly differentiated	very young, undeveloped
24.0	C_4	heart beating	young, some development
32.2	C_4	undifferentiated	ripe, gravid

different years. Further, the evidence at hand shows with virtual certainty that some individuals expel two batches of eggs within a single breeding season. The few crabs which mature a second batch of eggs near the close of the regular breeding season are probably the animals which participate in the off-season spawning during the winter months.

Hatching and Subsequent Growth

The multitude of empty egg capsules which adhere to each endopoditic seta of female exuviae indicates that hatching occurs while the eggs are adherent to the female. Ovigerous females in the captive environment of the laboratory had plucked most of the sponge prior to complete embryonic development. At the termination of the normal incubation interval, the floor of the aquaria was often covered with loose, viable ova. Near hatching time the exceedingly high mortality of these ova which had been removed by the female's chelae seems to indicate that the movement of the abdomen and the setae by crabs in the wild environment may actually aid in the hatching process of the prezoea from the enveloping capsule.

Hatching was observed microscopically. The investing membrane split about halfway around its periphery above the dorsal surface of the embryo; the prezoeae emerged dorsal side first in curled balls and soon began to move the appendages and to flex the abdomen. The prezoeae hatched in the laboratory were nonmotile. Most of the prezoeae underwent ecdysis the first day; others molted during the second day. The first zoeae were likewise immotile, and no subsequent larval development was obtained because of inadequate facilities. For an account of the zoeal stages of closely allied species, the reader is referred to Hart (1935).

The megalops stage of *P. crassipes* has been figured in outline fashion in Rathbun (1923, Pl. 34, Figs. 1 and 2) and in Johnson and Snook (1935, Fig. 305), but an adequate description has heretofore not been published. On March 8, 1941, several megalops of this species were collected at Carmel, California. Two of these were subsequently reared in the laboratory until the sixth crab stage, thereby definitely disclosing their identity. The collections were made by gently picking up rocks submerged in tide pools at a medium-high tide level (4.0 feet) and sweeping the surfaces with a soft brush while the rocks were submerged in a tub of sea water. Subsequently, the water was strained through a plankton net of coarse mesh. The transparency of specimens of the megalops stage makes it impractical to search for them on the rocks. The only clearly visible structures are the few chromatophores and the gastric mill. The megalopa crawl and swim readily. Swimming is accomplished by rapid abdominal movements similar to those of many macrurous species. The dactyli are furnished with long hook-like spines to facilitate the grasping of rock and algal surfaces.

The following account, together with a photograph of the megalops of *P. crassipes* (Pl. 2, Fig. 4), will fulfill the need for a description of this phase of the life history: length of carapace, 5.6 millimeters; width of carapace, 2.7 millimeters; almost transparent, slightly yellowish in color; scattered black chromatophores on the eyestalks, on the carapace above the gastric region, and around the intestine; three chromatophores on each merus of the ambulatory legs, two on each coxa, two on each propodus, and one on each dactyl; front wide, with center turned down to form the rostrum; chelae well developed; swimmerets broad and flattened with long plumose setae.

The megalops of *P. crassipes* may be distinguished from that of *H. nudus* and *H. oregonensis* by the greater size—nearly twice as broad and long as *H. nudus* and twice or more as broad and long as *H. oregonensis*. In addition, *H. oregonensis* has no plumose setae on the smoothly rounded posterior margin of the telson, whereas *P. crassipes* has two long, median setae and several shorter ones. Setae similar to those described above for *P. crassipes* are found on the telson of *H. nudus;* therefore, distinction between these two species must be made by size or by characters not mentioned here.

TABLE 11

SUMMARY OF THE GROSS GROWTH CHARACTERISTICS OF TWO CAPTIVE MALE SPECIMENS OF *P. crassipes* REARED FROM THE MEGALOPS STAGE.

STAGE	CARAPACE WIDTH (MM.) PRIOR TO ECDYSIS		CARAPACE WIDTH (MM.) AFTER ECDYSIS		SIZE INCREMENT IN MM.		PERCENTAGE SIZE INCREMENT		DAYS BETWEEN MOLTS	
	No. 1	No. 2	No. 1	No. 2	No. 1	No. 2	No. 1	No. 2	No. 1	No. 2
First crab	....	....	3.7	3.6	....	....	.....	.....	?	?
Second crab	3.7	3.6	4.5	4.4	0.8	0.8	21.7	22.2	14	20
Third crab	4.5	4.4	5.5	5.3	1.0	0.9	22.2	20.4	14	17
Fourth crab	5.5	5.3	6.4	6.1	0.9	0.8	16.4	15.1	20	16
Fifth crab	6.4	6.1	7.9	7.2	1.5	1.1	23.4	18.0	25	19
Sixth crab	7.9	7.2	10.1	8.4	2.2	1.2	27.8	16.7	26	31
Totals					6.7	4.8	111.5	92.4	99	103

The first crab stage of *P. crassipes* is likewise much larger than that of either *H. nudus* or *H. oregonensis*. It is nearly twice the width and length of *H. nudus* and more than twice the width and length of *H. oregonensis*. A description of the first crab stage of *P. crassipes* follows: carapace length, 3.7 millimeters; carapace width, 3.2 millimeters; front produced in two shallow lobes, unlike the straight frontal margin of the adult; the eyes proportionately very large, extending past the sides of the carapace; the two lateral teeth of the carapace distinct, and the thoracic striae characteristic of the species faintly indicated; the pereiopods provided with fine setae, both plumose and simple, with bands of dark and light areas along the ambulatory legs; the antennae and antennules proportionately larger and dissimilar to subsequent crab stages; the dorsal aspect of the animal containing minute chromatophores which impart a stippled effect.

The growth pattern of *P. crassipes*, from the megalops stage up to and including the sixth crab stage, was secured from observations on two captive crabs collected during the megalops condition. Both crabs were reared in large refrigerator dishes containing sea water from the locality in which they were collected. The mean monthly temperatures during the rearing period were: March, 14.8° C.; April, 15.3° C.; May, 15.8° C.; and June, 16.2° C. Food in the form of minute polychaete worms (*Mercierella enigmatica* Fauvel) was plentifully supplied. The data are summarized in Table 11. A remarkable constancy in total elapsed time with respect to the attainment of certain molt stages is immediately apparent. However, the variability in size increment (19.1 per cent) significantly contributes additional evidence concerning individual variation in growth discussed at some length on page 163.

THE TRANSITIONAL POSITION OF *P. crassipes* BETWEEN A LITTORAL AND TERRESTRIAL EXISTENCE

Specific and distinct habitats occur in all parts of the earth; but nowhere are they more apparent than along the seashore, where most littoral animals occur in horizontal zones within a vertically thin intertidal area. The high littoral zone occupied by *P. crassipes* is significant in this respect because its upper limit on the strand is adjacent to true terrestrial conditions; few species of the Brachyura range higher. Therefore, *P. crassipes* is a species which has almost acquired a terrestrial existence, and it occupies a position on the strand higher than that of most littoral crabs. Certain morphological transformations in this species, which are correlated with the attainment of a terrestrial habitat, have been studied by Pearse (1931). A physiological study by Jones (1941) on the osmo-regulatory features of this species has contributed additional evidence of its transitional character. The present investigation is concerned with several additional features which

are closely associated with the attainment of a terrestrial habitat. The results of these studies provide evidence to show that this species is one which is physiologically, morphologically, and behavioristically transitional between a purely marine and purely terrestrial crab.

It is generally acknowledged that adjustment to terrestrial conditions requires the ability to resist desiccation. In this regard it was shown earlier that, although 18 gills are present, the volume of the gills in relation to the volume of the body of *P. crassipes* is the lowest of any of the crabs tested (see p. 146). Pearse (1929*b*) has shown that crabs which are more highly adapted to a terrestrial life generally have fewer gills and these, by comparison, constitute a smaller percentage of total body volume. It was shown previously (see pp. 144 and 145) that this species withstands desiccation longer than closely allied but lower inhabitants on the strand. It was also shown earlier (see p. 184) that *P. crassipes* is found typically in places of greater temperature fluctuation than other crabs on the strand in central California. Although the desiccation tests fail to demonstrate a significant difference between *P. crassipes* and *H. nudus,* the latter species is invariably found in places of lower temperature. The high littoral position of *P. crassipes* unquestionably demonstrates its adaptation to a range of temperature fluctuations wider than that of the other littoral crabs of the region.

It has been pointed out that in the past the development of speed by animals has often been associated with aridity (Jehu, 1923). This hypothesis gains support from those crabs which have achieved the greatest success in conquering terrestrial existence. Relatively great speed is common to all land crabs in contrast to that of crabs of the lower littoral belt. To examine this hypothesis with respect to *P. crassipes,* the podomeric length of the second ambulatory leg of this species was compared with that of *H. nudus* (Table 12). Although all the podomeres of *P. crassipes* are longer than the corresponding ones of *H. nudus,* the two distal podomeres, especially the dactylus, show a proportionately greater difference in length than do the others. *P. crassipes,* therefore, is adapted morphologically for speed in a manner analogous to cursorial ungulates whose legs, especially the distal segments, exhibit a tendency to lengthen.

The regulation of osmotic pressure within the body is of great importance to marine organisms for entering terrestrial fresh-water habitats. Pearse (1931) has shown that crabs living continually in, or closely associated with, the ocean have the densest body fluids; those which live on land have the least saline fluids. Arthropods then, like vertebrates, in becoming adjusted to a life on land, lose some of the salt content of the blood. This loss suggests that such animals are developing mechanisms for maintaining the blood at a more or less constant salinity, regardless of changes in the surrounding medium. The salt content of the body

TABLE 12

A COMPARISON OF PODOMERIC LENGTH OF THE SECOND WALKING LEG BETWEEN SPECIMENS OF *P. crassipes* AND *H. nudus* OF EQUIVALENT CARAPACE BREADTH.

SPECIES	WIDTH OF CARAPACE (MM.)	MEASUREMENTS (IN MM.) OF THE SECOND WALKING LEG					
		I, II, III Coxa, Basis, Ischium	IV Merus	V Carpus	VI Propodus	VII Dactylus	Total
H. nudus	27.1	5.0	12.5	8.2	6.0	7.5	39.2
P. crassipes	27.1	5.7	13.9	8.6	7.7	8.8	44.7
Ratio of *P. crassipes* to *H. nudus*.....	1:1	1.14:1	1.11:1	1.04:1	1.28:1	1.15:1	1.13:1

fluids of *P. crassipes* is considerably reduced in comparison to brachyurans which range lower in the littoral belt (Pearse, 1931), but it is higher than that of crabs which have achieved a terrestrial or an almost terrestrial existence.

P. crassipes has achieved both hyperosmotic and hypoosmotic regulation (Jones, 1941). Therefore this species can regulate against the increasing salt concentration of the water in the gill chamber during periods of exposure to the air and can maintain a constant body salinity. A provision of this type is requisite to an active terrestrial existence. *H. nudus* and *H. oregonensis*, on the other hand, do not regulate hypoosmotically toward a salinity greater than that of the ocean water (Jones, *op. cit.*), a fact which discloses physiological evidence pertinent to their restriction to lower and more shaded positions on the strand. Both these species exhibit hyperosmotic regulation in brackish water to a greater magnitude than was found for *P. crassipes*. This condition partially explains why the latter species never occurs in water as brackish as that in which the two former species occur. Jones has shown, further, that hypoosmotic regulation occurs only among the Grapsidae and is exceedingly variable within the group, ranging from complete absence (*H. nudus* and *H. oregonensis*) to high development (*Uca crenulata*, and all land crabs).

Homeostasis is definitely correlated with the more highly advanced physiological grades found in the vertebrates among birds and mammals. Therefore it is not unreasonable to assume that stability of the internal physiological mechanism of arthropods is conducive to increased activity on the part of the possessor. Furthermore, those crabs which have highly developed hypoosmotic regulation (*Uca, Grapsus, Pachygrapsus*, etc.) have effected the greatest progress toward the conquest of the terrestrial habitat; hence they remain exposed to air for the greatest length of time.

Certain near-terrestrial Brachyura have evolved homing instincts reminiscent of purely terrestrial groups. *Ocypoda arenaria*, when molested, will return directly to its burrow from considerable distances (Cowles, 1908); the same was noted for fiddler crabs (Pearse, 1914). This behavior is unquestionably associated with their fossorial habit. Although *P. crassipes* does not burrow, several animals have been observed to wander short distances away from their base and later to return to the identical point of departure. To test the possibility of a homing instinct in this species, an experiment was devised in which 21 crabs were collected from a tide pool. The carapaces were marked with large numbers, and the crabs were released at four different loci 25 feet away from the pool. The releasing loci were selected to present four different types of routes home, varying from simple slopes to complex crevice formations. The crabs were released at night and observations were begun the following afternoon. Seven of the crabs were found back in the original pool; four of six releases deposited in difficult terrain returned; only two of five released on a moderately difficult terrain returned; and none returned from the locus separated from the pool by smooth, level rock. Several marked crabs were found in crevices near the releasing loci. It seems apparent, from the foregoing results, that homing behavior is nearly, if not totally, lacking in *P. crassipes*. The crabs seemed to be opportunists and secluded themselves in the best possible location. The crabs which returned to the tide pool probably found it during their usual nocturnal wandering.

Algal types which grow highest in the littoral belt may be significant in luring this species farther toward land. The abundance of this food, coupled with the fact that it forms the major portion of the diet, is unquestionably one of the reasons for the success of the species in maintaining itself in this relatively exposed area. It has been suggested by Pearse (1929*a*) that crabs become herbivorous as they approach terrestrial life; those which attain almost true terrestrial existence are entirely herbivorous. The crabs on the coast of central California are herbivores, with algae comprising the predom-

inant food supply; consequently this species adheres to the food type characterestically utilized by terrestrial species.

The reduction of gill volume relative to body volume, the ability to withstand desiccation, the eurythermal tolerance, the high locomotor development, the osmo-regulatory development, and the herbivorous food habits, all combine to substantiate the thesis that this species has progressed from a purely marine habitat toward a terrestrial existence. With these data at hand, it is possible to discuss with considerable assurance the route by which this species may be attaining a terrestrial life. Two routes to land are open: one via brackish to fresh water through estuaries and bays, and the other via the littoral area without first encountering decreased salinity. Inasmuch as hypoosmotic regulation is more highly developed than hyperosmotic regulation, it is certain that the adaptation to land has progressed through the littoral area rather than via the estuarine route, notwithstanding the occurrence of *P. crassipes* in the more saline areas of bays and estuaries. In contrast, the absence of hypoosmotic regulation, in conjunction with the highly developed hyperosmotic regulation, indicates that *H. nudus* and *H. oregonensis* are progressing toward a terrestrial existence via the estuarine route.

Barrell (1916) and Lull (1917) minimize the number of animals which have attained land directly through the intertidal zone; but, if we may judge from the multitude of species now partially adjusted to land, there must have been many in the past. Inasmuch as this species is attaining or has achieved morphological, physiological, and behavioristic adaptations which enable it to withstand the drier conditions attendant to a near-terrestrial habitat, and inasmuch as these adaptations coincide with those found in true land crabs, it is evident that this species, at the present time, has progressed toward a terrestrial existence via the littoral route.

Barrell (*op. cit.*) also maintains that the rarity of passage of crustaceans, gastropods, and vertebrates from a truly marine to a truly terrestrial mode of life through the apparently open path of the tidal zone, contributes evidence that an unused food supply could not alone operate as a cause sufficient to induce this change. However, the supposition that one or another factor is the primary cause for migration from sea to land is a somewhat limited point of view. The preservation of species depends upon the procurance of food, protection from enemies, reproduction, and continuous adjustment to continually changing environment; hence one lure is not sufficient cause for a migration of this magnitude. The utilization of algal types which occur high on the strand was only possible after the crab was adapted to it, so that their utilization did not interfere with other exigencies of life. *P. crassipes* has, then, made progress toward the attainment of a terrestrial habitat, the main prerequisites being aerial respiration, water conservation, swiftness, and internal stability.

SUMMARY

1. The present investigation of *Pachygrapsus crassipes* Randall, the lined shore crab, is concerned especially with its geographical and ecological distribution, intermolt cycle, molting, general habits and behavior, defensive mutilation and regeneration, predaceous and parasitic enemies, reproduction, and growth. In addition, information is advanced pertaining to the level attained by this species in the transition from a purely marine toward a terrestrial habitat.

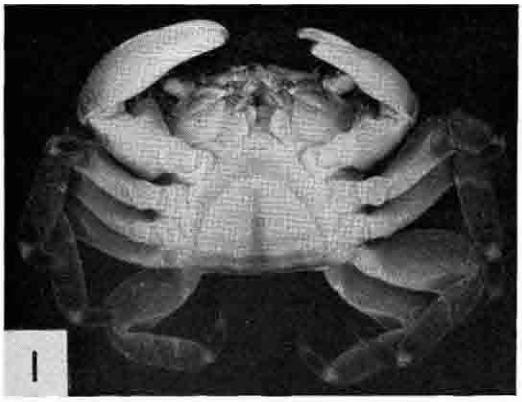
2. The authenticated geographical range of this species follows well-defined isotherms and extends along the western coast of North America from latitude 45° N. to latitude 24° N., and along the coast of Japan and Korea from latitude 37° N. to latitude 34° N. Probable avenues of dispersal to the Orient from America are discussed, and locality records outside the established range are considered.

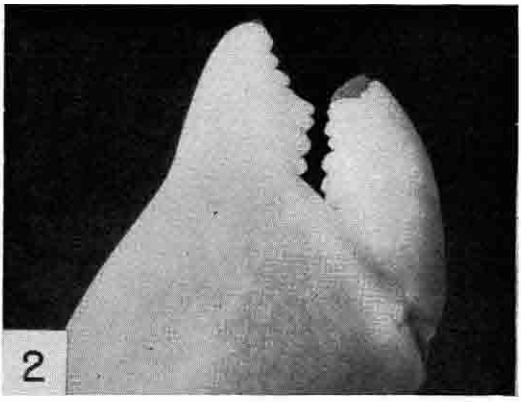
3. The general littoral habitat of *P. crassipes* includes three distinct biotopes. Each of these biotopes provides the fundamental ecological

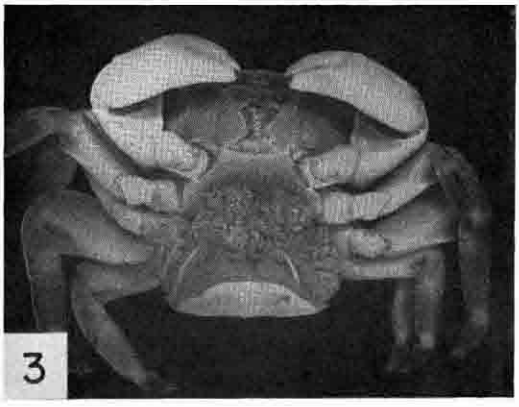
PLATE 1

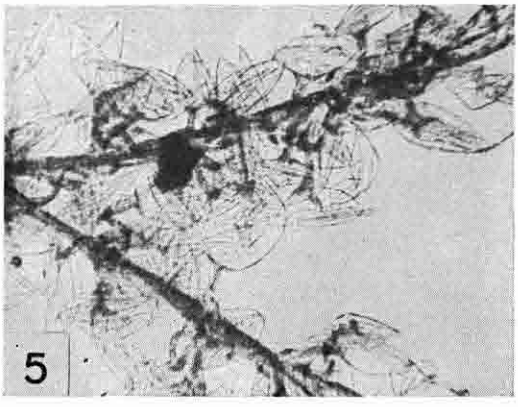
FIG. 1. A view of terrain type 1 at Pacific Grove, California. Note tide pool in foreground and numerous crevices.

FIG. 2. A view of the mud bank along Bolinas Bay. Note the holes in the bank which serve *P. crassipes* as refuge places. *Ulva lactuca* is abundant about the stems of *Salicornia* sp. shown above the vertical bank.









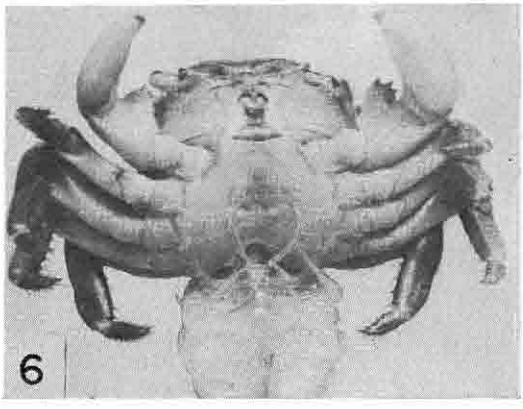


PLATE 2

FIG. 1. A photograph which indicates the comparative smallness of the newly regenerated cheliped (left side) after the first post-regenerational ecdysis.

FIG. 2. A photograph which shows the manner of papilla formation and regeneration of a dactyl located on a cheliped.

FIG. 3. A photograph which discloses the "sponge" of an ovigerous female. Note the comparative size of the ova, and the basket-like arrangement provided by the exopoditic and tergal setae.

FIG. 4. A photograph which shows the megalops of *P. crassipes* in dorsal view. Note particularly the comparatively large eyes and long ambulatory appendages bearing hooked dactylar spines.

FIG. 5. A photomicrograph which shows empty egg capsules attached to the endopoditic setae of the pleopods of a recent exuvia. Close examination will reveal the twisted funiculi.

FIG. 6. A photograph which shows the ventral aspect of a female crab with the abdomen extended. Note the vulvae near the mid-line of the sixth sternite and the four pairs of abdominal pleopods.

requirements of this eurytopic species, viz., a hard substrate containing refuge places, generally devoid of loose stones, sand, or mud, and possessing a more or less luxuriant growth of ulvaceous or filamentous algae. The interspecific relationship between the three grapsoid crabs which range on the highest littoral horizon are described with respect to morphological, physiological, and behavioristic differences.

4. A study of the seriation of morphological transformations during the intermolt cycle advances this knowledge to the grapsoid group. External morphological characters are designated as indicators of internal change. These characters should enable investigators to diagnose accurately the stages within the intermolt cycle. A framework upon which to base accurate observations on both experimental and behavioristic data is thereby provided. The utility of such criteria to disclose periodicity within a single intermolt interval is conclusively confirmed by an examination of several hundred wild specimens.

5. Exuviation is described in detail and its critical relationship to the life of the crab is made apparent. The incidence of molting is clearly demonstrated to be associated directly with the temperature of the water; the exuvial frequency is highest in summer months and relatively low from November to March. Post-exuvial expansion is nearly completed in 3 hours. The individual size increment after ecdysis is highly variable, and the percentage of size increment varies inversely with the initial size and the age. Comparative studies on the post-exuvial size increments of male and female crabs indicate that no significant variation occurs until an initial width of approximately 25 millimeters is attained. Thereafter, females exhibit a smaller post-exuvial size increment. Male crabs have been estimated to undergo 18 molts and females 21 molts before attaining maximum size, which is reached in a minimum of 3 years.

6. Visual, chemical, and tactile perception are well developed in this species. Odor has no stimulatory effect. When submerged food is sought, visual perception generally precedes either chemical or tactile, but chemical perception becomes predominant after a brief interval of time. Vision attains predominance during diurnal aerial activity; the tactile sense gains ascendancy after dusk. Although this species does not respond to sound vibrations within man's range, the tactile sense is a significant factor in regulating the activities of this crab.

7. This species is versatile with respect to directional locomotion, and is transitional between purely aquatic and terrestrial brachyurans with respect to speed.

8. *P. crassipes* may be designated essentially an herbivore, ordinarily a grazing herbivore, less commonly a plant scavenger, while facultatively a carnivore, chiefly an animal scavenger, and less often a predator.

9. Field data show that periodic changes in daily temperature, tides, exposure, and illumination have created a behavior pattern in these animals which seldom deviates from the standard and which approaches a monotony of repetitions.

10. The precocity and boldness of the young crabs of this species are probably attributable to their lack of experience and inhibitions, rather than to the relatively large, faceted eye-surface. The older and larger crabs with a greater faceted eye-surface indulge in the varied activities with more reserve and caution.

11. Advanced territorial relationships do not exist for *P. crassipes*. Refuges are defended but no individual forage areas are protected. There is no tendency toward social aggregation.

12. Defensive mutilation in this species occurs frequently and is easily achieved. The mechanism underlying this phenomenon is described in detail, and comparisons are made with other brachyuran species.

13. Experimental results show that a point is reached during the final synthesis of the integument (intermolt stage C_4) before which regeneration of a complete appendage will ensue prior to ecdysis, and after which regeneration is inhibited prior to ecdysis. Three suc-

cessive molts are required to bring a regenerating limb back to normal size. With the exception of the dactyl, regeneration from any point in the appendage other than the fracture plane has never been recorded in examinations of the several thousand crabs observed. Easy self-mutilation, rapid regeneration, and comparatively brief intermolt cycles apparently contribute greatly to the success of this species in reaching and establishing itself in an area rich in food materials, notwithstanding the fact that it is exposed to constant predation.

14. Predaceous enemies include gulls, rats, man, sea anemones, and, because of their cannibalistic tendencies, the crabs themselves. External parasites on this species are a rarity.

15. The usual brachyuran sexual dimorphism is present and the sexes appear in virtually equal numbers. Females were found to mature in 11 or 12 months, at which time they had a carapace breadth of about 15 millimeters. Male crabs are more precocious; mature males appear about 7 months subsequent to hatching, at which time they measure about 12 millimeters in carapace breadth.

16. Copulation and impregnation are described in detail. Most of the adult females become ovigerous between April and September; however, a few expel eggs during the winter months. Evidence seems conclusive that a portion of the females extrude two batches of eggs within a single breeding season. The incubation period requires approximately 1 month. The gross development of the incubating larvae and the behavior of the berried females are described.

17. The megalops stage of *P. crassipes* is described and compared with other closely associated grapsoid species.

18. An account of the growth of two carefully reared crabs from the megalops to the sixth crab stage shows considerable individual variation in growth and a remarkable constancy with respect to total elapsed time between the post-megalopal molt and the attainment of the sixth crab stage.

19. Morphological, physiological, and behavioristic adaptations exhibited by this species disclose that it has made progress toward the attainment of a true terrestrial habitat, because the main prerequisites (aerial respiration, water conservation, swiftness, and homeostasis) have been partially achieved. Further, these adaptations—osmo-regulation in particular—seem to indicate that the apparently open path from the ocean to a terrestrial habitat via the intertidal zone is being traversed.

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